

**Coastal Fog and Butterflies: How does microclimate  
impact butterfly habitat in San Francisco?**

A Thesis submitted to the faculty of  
San Francisco State University  
In partial fulfillment of  
the requirements for  
the Degree

Master of Arts

In

Geography

by

Sarah Elizabeth Gomes

San Francisco, California

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In this thesis we explore the relationships between coastal fog, the Coastal Green Hairstreak butterfly (*Callophrys viridis*) and the Seaside daisy plant (*Erigeron glaucus*). We address three broad questions: 1) How has the Green Hairstreak's habitat in San Francisco changed over time? 2) How do Green Hairstreak butterflies interact with Seaside daisy plants within their restored habitats? and 3) How does coastal fog influence the physiological function of Seaside daisy plants? Our results strongly suggest that coastal fog has a lasting impact on habitat quality. Our historical analysis shows that the Green Hairstreak butterflies are restricted to foggy coastal areas and that urbanization has negatively impacted their habitat. We observed that plant-butterfly interactions were influenced by microclimate conditions and plant characteristics, such as floral display and flower size. At the plant scale, we found that coastal fog enhances the physiological function of Seaside daisies (i.e., namely photosynthesis rates and stomatal conductance), which can help to alleviate drought stress. Finally, we use this information provide restoration recommendations which aim to improve habitat quality within the Green Hairstreak Corridor.

## **Preface and/or Acknowledgements**

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## **Chapter 1: Introduction**

### **Declining Biodiversity**

We are in the midst of a sixth mass extinction as a result of human activities (Kolbert, 2014) with climate change and habitat destruction as leading causes of biodiversity decline around the globe (Dirzo et al., 2014). Severe insect declines have been observed around the world (Goulson, 2019; Wagner et al., 2021). Wagner et al. (2021) describes the “insect apocalypse” as a “death from a thousand cuts” from stressors such as climate change, urbanization, agricultural expansion and pollution, among many others. Humans have fundamentally reconfigured plant-pollinator relationships, which have co-evolved for thousands of years, and weakened the ecosystem services that they provide (Burkle et al., 2013; Goulson, 2019; Wagner et al., 2021). Butterflies are considered “ecosystem indicators” because changes to butterfly communities can have cascading effects on entire food webs and overall ecosystem function; therefore, their presence or absence can indicate how well an ecosystem is functioning (Mukherjee et al. 2018). In order to protect butterflies in the future, it is critical that we first understand the resources and environmental conditions that they rely upon to persist.

### **The Scales of Butterfly Vulnerability**

Butterflies are particularly sensitive to small changes in their surrounding environment. Urbanization is a leading cause of butterfly population declines from habitat fragmentation and degradation (Blair & Launer, 1997; Bonebrake & Cooper, 2014; Casner et al., 2014; Clark et al., 2007; Soga & Koike, 2012). Urban areas have lower abundance, species richness, and diversity than rural areas (Blair & Launer, 1997; Casner et al. 2014), which leaves butterflies in urban areas more vulnerable to extinction than those in rural areas. Extinctions caused by landscape

fragmentation and habitat loss generally occur slowly compared to other causes, such as diseases (Soga & Koike, 2013). In areas of rapid urbanization, local extinctions occur more often than recolonization (Casner et al., 2014). However, there are practical solutions to mitigate butterfly extinctions in urban areas. By addressing the issue at various spatial and temporal scales, we can better understand butterfly vulnerability and implement such solutions.

### **Regional Scale**

There is an inverse relationship between human and butterfly populations, meaning that as human population density increases, butterfly populations typically decrease (Abbitt et al., 2000; Konvicka et al., 2006). Humans have a profound effect on butterfly communities through urbanization, and regional planning can either help or hinder their survival. Habitat disturbances from urbanization (i.e., defined as having more than half of a habitat modified by humans) have a negative impact on the species richness and abundance of butterflies (Kocher et al., 2000). Abbitt et al. (2000) identified the top hotspots for bird and butterfly vulnerability in the United States, classifying counties as “vulnerable” if they ranked within the top 5% for human population density and also contained restricted-range species. San Francisco was listed as one of California’s top hotspots for butterfly vulnerability (Abbitt et al., 2000), and it also happens to be a hotspot for biodiversity (Connor et al., 2002). Konvicka et al. (2006) also found a relationship between human density and butterfly vulnerability, further noting that the influence of a region’s economic history is important to consider because it speaks to the ways industrialization has shaped the landscape. For example, the Gold Rush in California sparked the rapid development of San Francisco (Delgado, 2009), which has contributed to the declines of several butterfly species (Shapiro, 2007; Tilden, 1956).

## Habitat Scale

Habitat fragmentation and isolation leads to decreased genetic diversity within butterfly communities (Collier et al., 2010). Clark et al. 2007 found that nectar resources, green spaces, and number of people had the most influence over butterfly diversity. Krauss et al. (2003) assessed habitat suitability by pairing butterfly survey data with landscape features, such as land-use type, habitat area, degree of isolation, and habitat quality; habitat area was the most important predictor of suitable habitat in specialist butterflies (i.e., butterflies with specialized food and habitat requirements), whereas landscape diversity was the most important for generalist butterflies (Krauss et al., 2003).

While green spaces in urban areas can certainly help to offset the effects of habitat fragmentation, not all green spaces can be utilized by butterfly populations. Chong et al. (2018) conducted a study to compare butterfly diversity within ( $\alpha$ -diversity) and between ( $\beta$ -diversity) localities in natural and artificial green spaces (e.g., lawns, turf grass, ornamental gardens, etc.). Cultivated areas had a weak positive relationship with species richness and had greater homogeneity that was likely driven by the loss of natural vegetation, i.e., replacing a natural meadow with lawn. The proposed solutions from this study echoed that of other studies: providing the right host and nectar plants is key to establishing healthy habitats in urban areas. Artificial green spaces can support butterfly communities, as long as they are cultivated with butterflies in mind by mimicking natural green spaces and including a range of food resources (Chong et al., 2018).

Gardens can provide refuge for vulnerable butterflies within the urban landscape, and the negative impacts of urbanization can be mitigated at a local scale by manipulating garden

characteristics. Di Mauro et al. (2007) studied how butterfly diversity was affected by garden size, number of flowering plants, and its surrounding matrix along an urban gradient (i.e., rural to suburban to urban). Medium and large gardens showed a decrease in diversity along this gradient (i.e., large gardens in rural areas had greater diversity than large gardens in suburban and urban areas, respectively) suggesting that surrounding matrix was only one of several factors influencing butterfly communities. Further, Fontaine et al. (2016) investigated which garden practices were most beneficial to urban butterflies by comparing several local and landscape variables. They concluded that garden size, nectar availability, and pesticide usage were the most important local factors in determining species richness and abundance of butterflies. Large gardens with high nectar offer that avoided pesticides had the greatest diversity and abundance (Fontaine et al., 2016). Therefore, manipulating these important garden characteristics can help to increase its benefit to urban butterflies.

### **Individual Scale**

Life-history traits are important species-specific predictors of a butterfly's vulnerability to urbanization. Many studies have shown that specialist butterflies are considered the most vulnerable; in fact, rare specialists decline twice as fast as common generalist species (Clark et al., 2007; Mukherjee et al., 2018; Soga & Koike, 2012). Soga & Koike (2012) determined that voltinism (number of flight seasons), food resource type, and matrix adaptability also determine vulnerability to urbanization, stating that specialist, uni-voltine, woody feeders with low matrix-adaptability were the most vulnerable. In addition, other studies have shown that size (measured by wingspan) is also important to consider, concluding that smaller butterfly species are less

persistent than larger butterflies (Bonebrake & Cooper, 2014). As a result, the vulnerability of butterflies varies between species, which is why species-specific studies are so valuable.

### **Microclimate and Butterflies**

Lepidoptera-focused conservation efforts often require managers to shift their idea of scale (Longcore & Osborne, 2015). Fine-scale elements like microtopography, microclimate, and phenological maturation are important to butterflies at all stages of life (Longcore & Osborne, 2015; Weiss et al. 1988). For this reason, it is crucial that habitat-scale restoration efforts first consider the fine-scale elements that influence individuals. Butterflies are considered ectotherms, because they do not generate their own heat and must get it from an outside source; as a result, thermoregulation is driven by immediate environmental conditions (Shapiro, 2007). Their thin and elegant wings contain cells which allow them to capture solar radiation and convert it into energy in order to fly (Shapiro, 2007). With that being said, their individual behavior on a day-to-day basis is largely dependent on weather conditions, with ideal flight on sunny days with little wind (Heer et al. 2013; Krauss et al. 2003; Lucas et al. 2013).

The timing of weather patterns has a lasting influence on butterfly populations. Microclimate influences the flowering phenology of nectar and host plants, which can impact the quality and availability of food resources as well as transitions between life stages (Weiss et al., 1988). Weiss et al. (1988) found that topography and microclimate were crucial in determining habitat quality of the Bay Checkerspot butterfly (*Euphydras editha bayensis*), concluding that solar radiation influenced larvae and pupae development; eggs laid early in the flight season showed increased survival, as larvae could persist on all slopes regardless of microclimate

differences; larvae from eggs laid later in the flight season showed decreased survival and were restricted to cooler slopes.

Butterflies seek microclimate protection during their dormant season as well, whether that be during diapause or their transformation from larva to adult. For example, Monarch butterflies (*Danaus plexippus*) seek out dense eucalyptus groves for their overwintering sites, which provide shelter from extreme weather conditions (Stuart Weiss, personal communication, October 21, 2021). Tracol et al. (2010) found that in a fog-influenced semi-arid shrubland, temperature was lower and relative humidity was higher under shrub canopies than in open areas, and that this distinction was more prevalent during extreme weather. Of the three shrubs included in their study (i.e., *Porlieria chilensis*, *Proustia cuneifolia*, and *Adesmia bedwellii*), the plant with the densest canopy (*P. chilensis*) provided the best protection from extreme weather conditions (Tracol et al., 2010). This type of protection is ideal for butterfly species which form their chrysalises underneath shrubs, such as the Coastal Green Hairstreak butterfly.

### **The Coastal Green Hairstreak Butterfly**

#### **Figure 1. Protected Butterfly Habitat – Marin Headlands**



*Figure 1 - View from protected butterfly habitat in the Marin Headlands (Golden Gate National Recreation Area), looking south towards the Golden Gate Bridge and San Francisco covered by coastal fog. (Photo Credit: Sarah Gomes)*

The Coastal Green Hairstreak (*Callophrys viridis*) butterfly is a small, iridescent green butterfly, native to coastal sand dunes along the coast of California. Their habitats include a diverse range of plants that are ideal for supporting Green Hairstreaks at all stages of life: larval food plants Coast buckwheat (*Eriogonum latifolium*) and Deerweed (*Lotus scoparius*), nectar plants such as Seaside daisy (*Erigeron glaucus*), Sea thrift (*Armeria maritima*), Beach strawberry (*Fragaria chiloensis*), and Yarrow (*Achillea millefolium*), along with other dune plants such as Dune tansy (*Tanacetum camphoratum*), Coastal sagebrush (*Artemisia californica*), California phacelia (*Phacelia californica*), and Dune knotweed (*Polygonum paronychia*) to name a few. Although they share similar habitat to their relative, the Inland Green Hairstreak (*Callophrys dumetorum*), the two species never co-occur; *Callophrys viridis* is considered a separate subspecies, restricted to the fog belt along the coast (Shapiro, 2007). Our research focuses entirely on the Coastal Green Hairstreak; any mentions of the shortened “Green Hairstreak” butterflies within this paper refer to *Callophrys viridis*. Coastal fog from the Pacific Ocean frequently inundates the areas where the butterflies reside and it is an important part of their coastal habitat (Fig. 1 & 2). Today, the butterflies are found within restored habitats in the Sunset District (Fig. 2) and Presidio of San Francisco, as well as nearby protected areas such as the Marin Headlands (Fig. 1) and San Bruno Mountain.

## Figure 2. Urbanized Butterfly Habitat – San Francisco



*Figure 2 - View looking north (toward Figure 1) from a restored Green Hairstreak habitat site within San Francisco, California, with fog rolling in from the Pacific Ocean to the west. (Photo Credit: Sarah Gomes)*

In San Francisco, the butterfly's sand dune habitat once covered the entire western half of the city (Fig. 2) but has been heavily developed over the past 250 years. The city of San Francisco has been so densely urbanized (Fig. 2) that this vulnerable butterfly was nearly extirpated and now exists in remnant patches of restored habitat that have been integrated throughout the city over the past two decades. There are a number of life-history traits which make this butterfly particularly vulnerable to changes in its environment. This small butterfly has a wingspan of approximately 20 to 25 mm (i.e., roughly the size of a nickel), is uni-voltine (i.e., only one short flight season, which typically lasts from late-February to mid-May), and is a specialist species with specific food and habitat requirements throughout all stages of life. For these reasons, it is among the most vulnerable of butterfly species to urbanization (Bonebrake & Cooper, 2014; Clark et al., 2007; Soga & Koike, 2012).

**Figure 3. Green Hairstreak Life Cycle on Coast Buckwheat**



*Figure 3 - Life cycle of the Coastal Green Hairstreak (*Callophrys viridis*) (i.e., a) adult, b) egg, c) caterpillar, and d) chrysalis stages) on its host plant, Coast buckwheat (*Eriogonum latifolium*). (Photo Credits: Sarah Gomes (a, c, and d), Luke Swanson (b), and Nature in the City (2016) (caterpillar and chrysalis - c and d))*

The Green Hairstreak's four life stages primarily revolve around its main host plant, Coast buckwheat (*Eriogonum latifolium*) (Fig. 3). Female adult butterflies (Fig. 3a) disperse eggs throughout their habitat on the underside of Coast buckwheat leaves (Fig. 3b), laying only one egg at a time. Eggs are roughly 0.5 mm in size and hatch after only one day. Caterpillars will experience five instars, in which they grow from 2 to 15 mm in size, changing their coloring with each transition to mimic the colors of the Coast buckwheat plant (Fig. 3c). During this stage, caterpillars feed from the leaves and flowers of their host plant (Fig. 3c). At the end of its fifth instar, the caterpillar crawls underneath the host plant to form a small brown chrysalis (Fig. 3d) for the remainder of the year (i.e., roughly nine months). The plants' dense under-canopies serve as microrefugia for dormant chrysalises, providing warmth and shelter from the elements and

other disturbances (Fig. 3d) (Tracol et al., 2010). The following spring, butterfly emergence is controlled by environmental factors and requires at least three consecutive days of heat (i.e., above 65°F). In the early spring, when winter rains have subsided and the weather is warm, each small iridescent green butterfly will emerge from its chrysalis, ready to mate and begin the cycle again (Fig. 3a). The flight season lasts for two to three months, but each individual butterfly only lives for roughly two weeks (Liam O'Brien, personal communication, July 19, 2019).

#### Figure 4. Nectar Resources

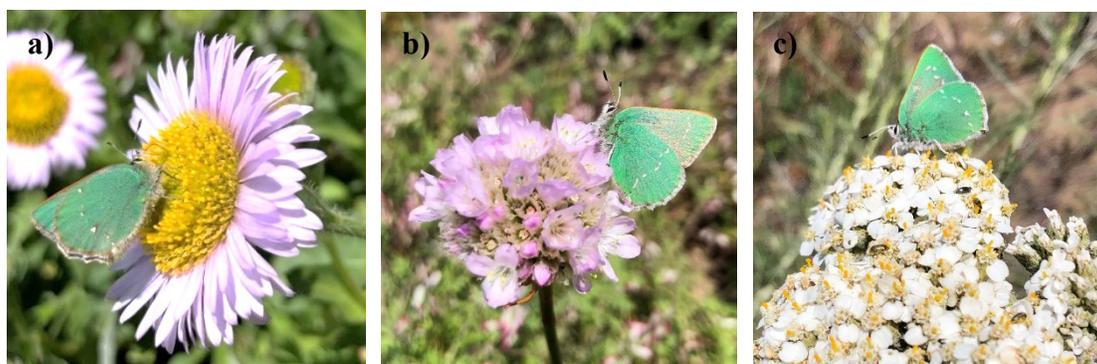


Figure 4 - Adult Coastal Green Hairstreak butterflies feeding from a) Seaside daisy (*Erigeron glaucus*), b) Sea thrift (*Armeria maritima*), and c) Yarrow (*Achillea millefolium*). (Photo Credits: Sarah Gomes)

Although the majority of their life cycle revolves around the Coast buckwheat plant, nectar from flowering plants is their primary food source that sustains them as adults. Green Hairstreak butterflies typically feed from a variety of nectar resources, such as Seaside daisy (Fig. 4a), Sea thrift (Fig. 4b), Yarrow (Fig. 4c), Beach Strawberry and many others, although they tend to visit Seaside daisies frequently. In the adult stage, butterflies take all of the crucial actions that shape the next year's population: foraging for food, finding mates, laying eggs, etc. A healthy balance of nutrients from different nectar plants increases both their lifespan and the number of eggs they can lay (Rani & Raju, 2016). Several studies have shown that nectar resources are among the most important predictors of genetic diversity and butterfly success

within urban habitat patches (Di Mauro et al., 2007; Fontaine et al., 2016). Additionally, it is known that butterflies have the potential for short-term learning; often times they will remember and re-visit highly rewarding nectar plants (i.e., at both the species and individual plant scales) (Shapiro, 2007). For these reasons, we chose to study the Green Hairstreak butterflies in their adult form, focusing on how they interact with nectar plants to make inferences about habitat quality.

### **Objectives**

The Coastal Green Hairstreak and their host and nectar plants have co-evolved in foggy coastal habitats, and their distribution is restricted to the coastal fog belt, so fog must be important to their survival in some way. In this thesis we aim to understand how microclimate, more specifically coastal fog, impacts habitat quality. We explore the relationships between coastal fog, the Seaside daisy plant, and the Coastal Green Hairstreak butterflies within restored butterfly habitats in San Francisco. We address the issue of habitat quality across various scales of time and space, focusing on historical biogeography (macroscale), plant-butterfly interactions (mesoscale), and plant function (microscale) to address three broad questions: 1) How has the Green Hairstreak's habitat in San Francisco changed over time? 2) How do Green Hairstreak butterflies interact with Seaside daisy plants within their restored habitats? 3) How does coastal fog influence the physiological function of Seaside daisy plants? When pieced together, this information tells us how coastal fog might influence habitat quality as well as the butterfly's distribution and behaviors. We hypothesize that coastal fog has a lasting impact which improves overall habitat quality from increased plant function, and this information may be used to

provide restoration recommendations to improve habitat quality for the Coastal Green Hairstreak butterfly.

## Chapter 2: Historical Biogeography

To truly understand butterflies, we must first untangle a web of interactions between the butterfly and its habitat through time and space. While the subject of studying butterflies seems, at first, purely physical, it is important to also consider the social aspects that shape their existence. Butterflies have several important ecological and cultural roles. From ancient times until today, many cultures around the world share the belief that butterflies represent the souls of our ancestors (Johnson; Kritsky & Cherry, 2000; Manos-Jones, 2000). For example, the Ancient Greek word for “butterfly” (*psyche*) is the same word for “soul,” which is also true in other cultures (Kritsky & Cherry, 2000; Manos-Jones, 2000). Butterflies are prominent symbols in insect mythology, most commonly associated with metamorphosis and the rebirth of the soul in the afterlife (Kritsky & Cherry, 2000). Whether or not we believe this to be true, modern science has detected consciousness, and even personalities, in insects; this suggests that insects have a sense of self and therefore subjective experiences (Baron & Klein, 2016; Marris, 2021). Attempting to view the world through their eyes provides a unique perspective and an opportunity to connect to their stories on a more personal level. When we try to see the world from the eyes of these magnificent creatures, we may find they are more like our own selves than we’d previously realized. When we see how far they’ve come, what they’ve endured to exist today, we may also find inspiration that compels us to protect them further.

In short, the butterfly is a symbol of transformation and immortality of the soul – a fitting metaphor for the story we aim to tell. The Green Hairstreak butterflies lived through every major historical event in San Francisco and continue to do so today, adapting to change as the passage of time requires. In this chapter, the resilient Green Hairstreak butterflies are our glimpse into the

past. We have ample proof that, like us, these butterflies are conscious beings, with their own point of view (Marris, 2021). In this section we will travel back in time, through the eyes of a Green Hairstreak butterfly, to understand changes in environmental history so that we can better understand their distribution and behaviors today. Using archival research methods, we reconstruct their history using historical photos, maps, museum specimens, descriptions and field notes to follow the Green Hairstreak through time, with context to major historical events that shaped urban development in San Francisco.

### The History of Green Hairstreaks in San Francisco

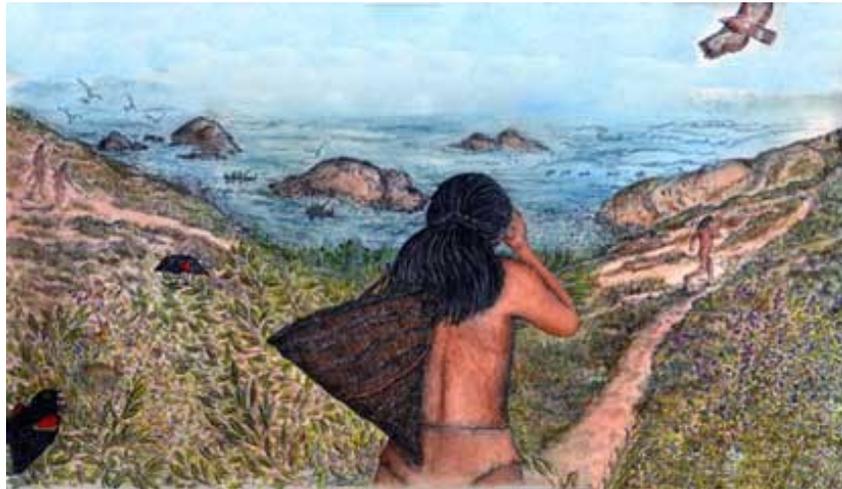
**Figure 5. The Ecology and Natural History of San Francisco: Wild in the City Map**



Figure 5 - Comparison of San Francisco before 1750 to 1990, titled "The Ecology and Natural History of San Francisco: Wild in the City" by Nancy Morita (1992). Left column of legend reads "sand dune," "grassland," "coastal scrub," "freshwater creek," and "saltwater marsh." Right column of legend reads "Ohlone village," "Ohlone seasonal camp/artifacts," "native habitat," "native habitat," and "topography."

Now restricted to only small patches of remnant habitat, the Green Hairstreak once occupied expansive tracts of the San Francisco Peninsula. Before development, sand dunes sprawled across the western half of the city and stretched eastward into grassland and coastal shrubland habitats before reaching the San Francisco Bay (Fig. 5). The San Francisco Bay Area has always been well known for its rich biodiversity, and even today, it is still a major biodiversity hotspot, despite the many changes that have occurred over the last two centuries (Fig. 5) (Connor et al., 2002). Early explorers described their shock at the abundant diversity of life, which had existed here for thousands of years alongside the indigenous Ohlone people (Margolin, 1978). In a time when grizzly bears roamed freely and mountain lions, coyotes, birds, fish, insects and other creatures were abundant, the Ohlone peoples lived more closely linked with nature than we do today. They worshiped the spirits of animals and wove them into their culture, incorporating their movements into dances and other art forms (Margolin, 1978). Of the Ohlone peoples, the Yelamu tribe lived in present-day San Francisco within several villages, the locations of which anthropologists have been able to identify through artifacts and historical records (Fig. 5) (Morita, 1992; Solnit, 2010). Unfortunately, none of the myths and legends specific to the Yelamu tribe are known today because of disease, displacement, and poor documentation by Spanish missionaries upon colonization in the late 1700's and early 1800's (Solnit, 2010). Nonetheless, the Ohlone people and their culture live on, giving us insight into what life was like before colonization.

**Figure 6. Ohlone Along the Coast**



*Figure 6 – Indigenous Ohlone people along the coast, looking out at the Pacific Ocean (Source: National Park Service, 2020)*

Although there is no clear documentation of Ohlone butterfly legends, the indigenous people of the area must have interacted with the Green Hairstreak due to their location on the coast (Fig. 6). The Yelamu most often established settlements along the eastern side of the peninsula, along waterways where microclimates were ideal and resources were plentiful (Solnit, 2010). They established a permanent village (Ompuromo) near present-day Lake Merced, on the southern end of the butterfly's sand dune habitat, and placed seasonal encampments nearby (Fig. 5). Ethnobotanical evidence shows that the Ohlone used the butterfly's host plant, Coast buckwheat, for food and medicinal purposes. They created decoctions of Coast buckwheat roots, stems, and leaves to be used as remedies for coughs and colds as well as pain relief (Bocek, 1984). Coastal tribes north of San Francisco, such as the Round Valley tribe of present-day Mendocino, used Coast buckwheat for similar medicinal purposes and also reported that it was a tasty treat sought after by children (Chestnut, 1902). Although it is unclear whether the Yelamu people directly cultivated Coast buckwheat, it is known that many native peoples used sustainable harvesting practices which increased plant health over time (Kimmerer, 2013).

**Figure 7. Traversing Butterfly Habitat on the Anza Expedition, 1776**

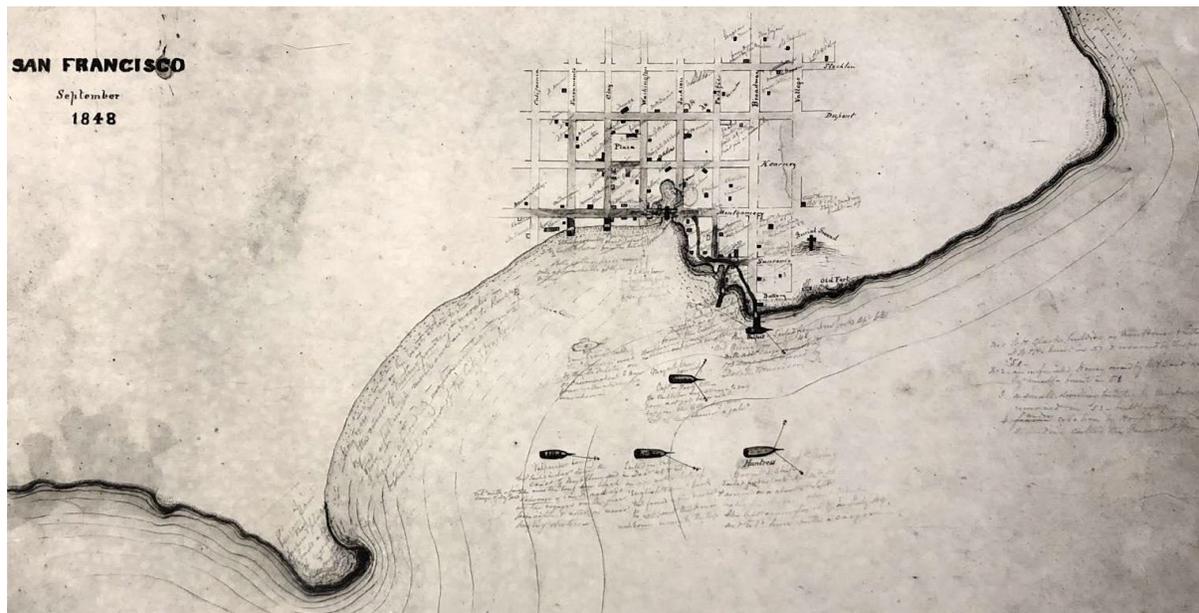


*Figure 7 - Painting "San Francisco Bay" by David Rickman (2007) depicts Spanish explorers during the Anza Expedition of 1776 overlooking the port of San Francisco (Source: East Bay Regional Park District PDF – Anza Expedition of 1776)*

The arrival of Spanish explorers quickly changed the dynamics between humans and nature, and began to disturb and extirpate populations that had co-existed long before European contact (Margolin, 1978). Urbanization began in the mid 1700's when Spanish explorers, seeking domination of the Americas and the Pacific trade route, began to colonize the area to develop trade routes and to establish missions and military defenses (Delgado, 1996). Father Pedro Font, Spanish missionary of the Anza Expedition, reported their arrival in San Francisco on March 27, 1776 in his diary, in which he kept daily notes as they explored the San Francisco Bay Area (Font, 1913). Though there is no direct record of butterfly sightings in his journal, nor relevant illustrations, it is clear that the areas colonists occupied overlapped with Green Hairstreak habitat of the coastal bluffs. As the expedition traversed the Green Hairstreak's coastal habitat (Fig. 7), Font describes the stark contrast between the crashing waves along the

Pacific Coast and the calm waters of the eastern bayfront, as well the sand dunes along the coast and the differing colors of the rocky cliffs of the port (Font, 1913). At the time, the Spanish descriptions of the area primarily focused on resources for settlements and encounters with indigenous peoples; not many Spaniards were studying insects or plants, and naturalists would not accompany expeditions until the 19<sup>th</sup> century (Ordeman, 2011). For the next several decades, the Spanish would continue to modify the landscape through agriculture and the development of the Presidio, but the coastal sand dunes remained mostly untouched by development.

**Figure 8. Yerba Buena Cove Before the Gold Rush – 1848**

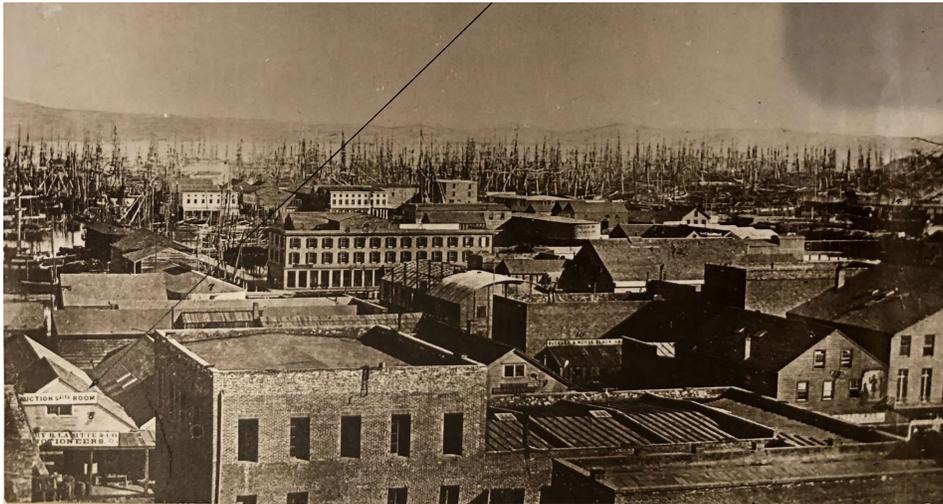


*Figure 8 - Map of San Francisco in September, 1848, drawn by Captain August Harrison. (Source: Notes on the Gold Rush Ships, San Francisco Maritime Museum)*

In the early 1800's, California came under Mexican rule and San Francisco was known as Yerba Buena. Mexico released its ownership of the land to the United States in 1846, only two years before gold was discovered in 1848 (Bacon, 2013). Prior to this discovery, Yerba Buena was a small village of around 400 people (Delgado, 2009) most valued for its location along the

coast, which made it a prime location for trade. The land itself proved to be difficult to settle due to the hilly terrain, foggy weather, and unfavorable living conditions (Dow, 1973). Covered in sand dunes, chaparral, and rocky outcroppings, its steep slopes were not ideal for building a city. Most of the population lived on the hillside above Yerba Buena Cove (Fig. 8), which extended from south to north from Rincon Point to Clark's Point, underneath the present-day Financial District. Captain August Harrison, master of the BELFAST brig, illustrates this in his map of San Francisco in September 1848 (Fig. 8).

### **Figure 9. The Buried Ships of San Francisco**



*Figure 9 - Ships filling Yerba Buena Cove. (Source: Notes on the Gold Rush Ships, San Francisco Maritime Museum)*

The discovery of gold began an era of mass global movement, sparking the rapid and unprecedented transformation of San Francisco. In a matter of months, Yerba Buena transformed from a village to a city, a place that people all around the world were dreaming of. James W. Marshall discovered gold in January of 1848, just 130 miles from San Francisco, eleven months before president James Knox Polk announced the discovery in December of 1848 (Bacon, 2013). The news spread like wildfire - tens of thousands of people packed their bags and headed for San

Francisco in the hopes of striking gold and a fresh start. The population boomed from 2,000 people in February, to 3,000 people by March, to 5,000 people by July of 1849. By the spring of 1850, the city housed about 40,000 people (Delgado, 2009). Over the course of two years, more than a thousand ships filled Yerba Buena Cove (Delgado, 2009). So few people were seeking returning passage that ships began to gather in the harbor (Fig. 9). Ship owners realized that by anchoring their ships they could lay claim to the land underneath, and transformed them into floating buildings – mostly warehouses, but also hotels, saloons, offices, or prisons (Delgado, 2009). Around fifty of these abandoned ships still lie buried beneath the Financial District. As the population continued to grow, development that began near the eastern waterfront quickly moved west and sprawled across the land (San Francisco Maritime Museum).

### Figure 10. Early Green Hairstreak Specimens



Figure 10 – Coastal Green Hairstreak (*Callophrys viridis*) specimens from the California Academy of Sciences (CAS) Entomology Collections. (Photo Credit: Sarah Gomes)

Naturalists, botanists, and entomologists were among the many immigrants to San Francisco in the early 1850's. They began to collect and study the native plants and butterflies in the city, including Green Hairstreak butterflies. Before the California Academy of Sciences (CAS) was established, collectors sent their specimens to institutions on the East Coast, such as the National Museum of Natural History. In the spring of 1853, the CAS was established in San Francisco to house the rapidly expanding specimen collection (Ordeman, 2011). This led to some confusion about species records. As lepidopterists from around the world arrived in San Francisco and began classifying and identifying butterfly species, some specimens were mistakenly identified as "new" species because the collector had not realized the species had already been identified (Brown & Opler, 1970). This sparked a taxonomic debate about the proper scientific name for the Coastal Green Hairstreaks of the San Francisco region, creating confusion that persists today. There have been several debates to settle the score on the correct term for the Coastal Green Hairstreaks found here (Emmel et al., 1998; Scott et al., 2010; Shapiro, 2007). They most recently determined *Callophrys "viridis,"* designated by W. H. Edwards in 1862, (rather than "*dumetorum*" or "*sheridanii*") as a distinct subspecies from San Francisco (Scott et al., 2010). This confusion makes historical analyses difficult, particularly for specimens of the mid 1800's. Further, most of the San Francisco butterfly records from the late 1800's and early 1900's were destroyed by the 1906 earthquake and subsequent fires, and so are unavailable for our review today (Ordeman, 2011). Instead, we rely on the works of others who have attempted to untangle the taxonomic web of Green Hairstreak specimens from prominent lepidopterists of the time, such as William Henry Edwards and Hans Hermann Behr (Brown & Opler, 1970), as well as descriptions and specimens from later time periods (Fig. 10).

**Figure 11. Urban Sprawl in 1878**



*Figure 11 - Bird's eye view of San Francisco in 1878, looking south-west from the San Francisco Bay.*

Rapid growth in population from the Gold Rush required rapid development. Businesses were built upon buried ships, roads were reconstructed again and again, and the city quickly sprawled inland from the north-eastern shoreline (Fig. 11). In the decades to follow, the urbanization that began at the San Francisco Bay waterfront expanded across the city to reach the modern-day Sunset District, modifying the Green Hairstreak's extensive sand dune habitat (Fig. 11).

**Figure 12. Views of Ocean Beach - 1865 and 1890**



*Figure 12 - View of Ocean Beach from Cliff House in 1865 (left) and 1890 (right), looking east toward the hills (Source: San Francisco History Center, San Francisco Public Library)*

The development of Golden Gate Park marked the beginning of urbanization of the sand dunes along the western half of the city. In 1870, the city of San Francisco acquired over 1000 acres of land to create a park to rival New York's Central Park. The park would soon house attractions such as the Conservatory of Flowers, Botanical Garden, zoo animals and open spaces for large gatherings, attracting visitors from all over the world. As traffic increased to the park, so did the development of the sand dunes. By 1890, development had reached the Pacific Coast and the Sunset District had begun to change. Construction stretched along the Great Highway and visitors flooded Ocean Beach (Fig. 12), marking the beginnings of the dense development of the Sunset District.

**Table 1. CAS *Callophrys viridis* Collection**

Table 1 - Number of *Callophrys viridis* specimens from San Francisco, per decade, in the California Academy of Sciences (CAS) Entomology Collection, accessed on June 29, 2021. Footnotes list collector names.

Number of Specimen Collections ( <i>Callophrys viridis</i> ) – California Academy of Sciences									
Location	1900's	10's	20's	30's	40's	50's	60's	70's	80's
San Francisco (unspecified)	3 <sup>a</sup>			1 <sup>b</sup>	1 <sup>b</sup>	19 <sup>cd</sup>			
Presidio			5 <sup>b</sup>	4 <sup>b</sup>		5 <sup>e</sup>			
Fort Funston			2 <sup>b</sup>						
Lone Mountain		19 <sup>a</sup>							
Grandview Park									1 <sup>h</sup>
Lake Merced							1 <sup>g</sup>		
Glen Park						1 <sup>e</sup>			
Twin Peaks						1 <sup>e</sup>			
San Miguel Hills							1 <sup>f</sup>		

<sup>a</sup>F.X. Williams <sup>b</sup>L.I. Hewes <sup>c</sup>R. Wilson <sup>d</sup>J.W. Tilden <sup>e</sup>D. Giuliani <sup>f</sup>D.C. Rentz <sup>g</sup>T.W. Davies <sup>h</sup>R.L. Langston

**Figure 13. General Locations of CAS Specimens**

Figure 13 - Locations of CAS specimens from Table 1 and other mentioned neighborhoods.

The CAS has an extensive entomology collection with several drawers of Green Hairstreak (*C. viridis*) specimens, many of which were collected in the western half San Francisco (Table 1 and Fig. 13). These butterflies are distinctly coastal, and their distribution

appears to be linked to fog. No records indicate that Green Hairstreaks were found on the eastern shoreline, which we presume is due to its different microclimate conditions (i.e., less foggy and not exposed to the coast). Other locations included San Bruno Mountain, Monterey, and Santa Cruz; although, for the sake of this story, specimens from other locations are not included in this analysis. The earliest *C. viridis* specimen included in our analysis was collected in 1905 by F.X. Williams with an unspecified location within San Francisco. Although it appears that there were only 3 specimens collected in the early 1900's (aside from specimens destroyed by the fires following the 1906 earthquake), we know they still remained in the city during this time (Table 1).

**Figure 14. Sunset Sand Dunes – 1910**

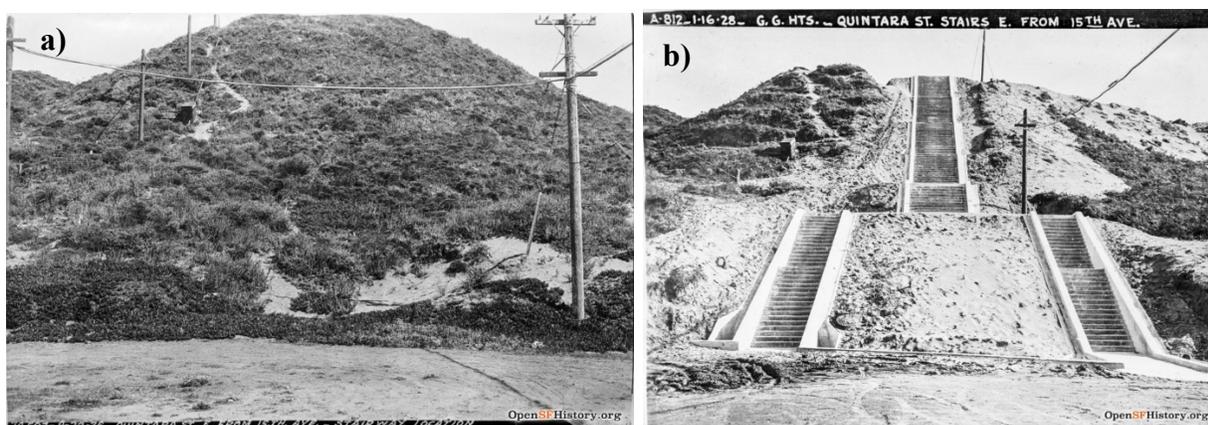


*Figure 14 - Colorized images of sand dunes in the Sunset District circa 1910, looking west toward the Pacific Ocean (Source: OpenSFHistory / wnp27.3306 and OpenSFHistory / wnp27.3305)*

In the 1910's, much of the inland dune habitat still remained despite the development around Ocean Beach (Fig. 14), and lepidopterists continued to contribute specimens to the CAS for several decades to follow. The collection contains 19 *C. viridis* specimens from the 1910's that were collected in the Lone Mountain neighborhood (Table 1), which is situated further inland from the Sunset District in a mixed sand dune and grassland habitat, but still exposed to

similar local climate conditions. Entomologist, Frances X. Williams includes the Green Hairstreak in his article on declining butterflies in San Francisco in 1910, noting that it was “a common insect occupying a considerable area in the western portion of the city” at the time, although he noted the diminishing sand dune habitat in his introduction, as well as the insect declines that followed (Williams, 1910). He describes, in great detail, the characteristics and behaviors of Green Hairstreak butterflies through all life stages, based on observations of collected living specimens, contributing greatly to our knowledge of the butterfly’s life cycle (Williams, 1910).

**Figure 15 – Building Quintara Steps**



*Figure 15 - Photographs taken before (a) 1926 and during (b) 1928 the construction of Quintara Steps, at the intersection of 15th Ave and Quintara St. (Sources: a) OpenSFHistory / wnp36.04420.jpg and b) OpenSFHistory / wnp36.03604.jpg)*

Throughout the Sunset, large habitat patches were destroyed to make room for the growing human population. The above images (Fig. 15) showcase the construction of Quintara Steps, which today support the Green Hairstreak’s most abundant population in San Francisco (iNaturalist, 2022). The site was prime butterfly habitat before completion of the steps in 1928 (Fig. 15a) and would soon be surrounded by residential homes. Such rapid change was occurring all along the Sunset District, quickly fragmenting and degrading butterfly habitat in its wake.

**Figure 16. Urbanization of the Sunset District (1920's – 1950's)**



Figure 16 - Urbanization of the Sunset District, with four images each roughly 10 years apart: in 1928, 1936, 1946 and 1958 (Sources: top left, OpenSFHistory / wnp36.03602.jpg; top right, OpenSFHistory / wnp36.10078.jpg; bottom left, OpenSFHistory / wnp26.201.jpg; bottom right: OpenSFHistory / wnp28.3734.jpg)

The development of the Sunset District continued in the 1920's and the decades to follow (Fig. 16), sparking a dramatic decline in Green Hairstreak butterflies. Most of the Outer Sunset was thoroughly developed before 1950, with the largest expansion between 1935 and 1945 (Fig. 16) (Brown, 2013). In the 1920's, CAS specimens were collected from the Presidio and Fort Funston (Table 1). In the 1930's, 4 specimens were collected in the Presidio and one in an unspecified location in San Francisco (Table 1). Only one CAS specimen was collected in the 1940's (Table 1). *C. viridis* is a lesser-known butterfly that shared the same habitat – and nearly the same fate – as other famous butterflies such as the Xerces blue (*Glaucopsyche xerces*), which

would vanish from the Sunset in the 1940's, and later be recognized as one of the first species to go extinct from urbanization in North America. In the following decade, entomologist James W. Tilden remarked, "Only a few years before, [the Xerces blue] had been the most characteristic butterfly of the coastal sand dune area known as the Sunset District, but complete settlement of the area left it no habitat to inhabit." (Tilden, 1956). The Green Hairstreak faced the same struggle in the 1940's, but continued to persist in small numbers, possibly because its host plant, *Eriogonum latifolium*, was less sensitive to disturbances than the *Lotus (Hosackia)* favored by Xerces blue (Tilden, 1956).

Tilden collected several specimens from an unspecified San Francisco location in the 1950's; other collectors donated specimens collected in the Presidio, Glen Park, and Twin Peaks areas (Table 1). In 1956, Tilden observed in his paper "San Francisco's Vanishing Butterflies" stating that "Like the other San Francisco butterflies, *viridis* is engaged in a losing struggle with man's encroachment." (Tilden, 1956). By 1958 the sand dune habitat that once covered the Sunset District had nearly disappeared (Fig. 16).

This decline was also evident in the CAS collection, which contains only two specimens from the 1960's in the Lake Merced and the San Miguel Hills; none were collected in the 1970's, and only one specimen in 1981 at Grandview Park in the Golden Gate Heights neighborhood, the most recent *C. viridis* specimen in the CAS collection (Table 1). Very few sightings were reported by lepidopterist Barbara Deutsch in the 1980's; although the Green Hairstreak was considered by some to be extirpated (i.e., locally extinct) in the area, the butterflies still existed in small numbers at that time (Laura Castellini, personal communication, April 16, 2021; Liam O'Brien, personal communication, March 28, 2022).

**Figure 17. Remaining Population at Rocky Outcrop**



*Figure 17 - View of Rocky Outcrop, where a remaining Green Hairstreak butterfly population was discovered by local lepidopterist, Liam O'Brien. (Photo Credit: Sarah Gomes)*

While sitting on a rocky outcropping overlooking the Sunset (Fig. 17), local lepidopterist Liam O'Brien discovered a small remaining population of Green Hairstreak butterflies in 2006 (Liam O'Brien, personal communication, July 19, 2019). O'Brien had set out to inventory the butterflies of San Francisco and discussed his plans with Deutsch, one of the lucky few to have seen the Green Hairstreaks after their decline. Deutsch told O'Brien of her findings, which prompted his search to document the remaining population (Liam O'Brien, personal communication, March, 28, 2022). Inspired by the butterfly's persistence, O'Brien suggested restoring a habitat corridor filled with the butterfly's host plant to the local non-profit organization, Nature in the City. In 2007, Nature in the City, O'Brien and other partners began to

establish the Green Hairstreak Corridor within the Golden Gate Heights neighborhood (Amber Hasselbring, personal communication, May 1, 2021).

The Green Hairstreak Corridor is a network of 11 stepping-stone habitats in the Golden Gate Heights neighborhood (Fig. 18). Restoration sites were strategically placed, roughly 200 feet apart from one another, in an attempt to connect the two remaining populations in the Presidio and Hawk Hill (Amber Hasselbring, personal communication, May 1, 2021). In addition, Nature in the City has worked closely with neighbors to plant native habitat in their backyards and gardens between sites. The Green Hairstreak Corridor has been a continuous effort over the past 15 years, made possible with the help of countless volunteers and neighborhood site stewards. The habitats have been planted with the butterfly's host plant and a variety of nectar plants carefully chosen to support Green Hairstreak butterflies and other pollinators, with a total of 910 different species reported throughout the Corridor (iNaturalist, 2022). With the help of modern technology, recent Green Hairstreak sightings are automatically gathered within the Green Hairstreak Monitoring Project on iNaturalist, which illustrates their distribution throughout the Green Hairstreak Corridor. At present, iNaturalist records show that, over the past 12 years, Green Hairstreak butterflies have been seen at all restored sites, with the exception of 12<sup>th</sup> & Pacheco (iNaturalist, 2022), perhaps due to its location on the eastern (inland) slope. The butterflies are most abundant on the Quintara Steps (Fig. 18b), Rocky Outcrop (Fig. 18d), and Grandview Park (Fig. 18a), with the highest number of sightings at Quintara Steps each year (iNaturalist, 2022). It is not currently understood why the butterflies favor Quintara Steps, though we explore this concept in later chapters.

**Figure 18. Restored Habitats of the Green Hairstreak Corridor**



*Figure 18 - Six of eleven restored habitats within the Green Hairstreak Corridor: a) Grandview Park, b) Quintara Steps, c) 12th & Pacheco, d) Rocky Outcrop, e) Hawk Hill, and f) 14th & Pacheco (Photo Credits: Sarah Gomes)*

**Figure 19. Baker Beach**



*Figure 19 - Remnant butterfly habitat at Baker Beach, along the Pacific Coast (Photo Credit: Sarah Gomes)*

Aside from in the Green Hairstreak Corridor, iNaturalist records also show Green Hairstreak butterflies in other remnant habitats within the city, especially at restored habitats within Golden Gate National Recreation Area such as Baker Beach (Fig. 19) and the Presidio.

In Fig. 19, we view the landscape that the Spanish laid eyes on 248 years ago (Fig. 7) through a different lens. We see the peaks and troughs of the Green Hairstreaks' history, along with the Golden Gate Bridge – an iconic symbol of the historic development that changed the landscape and the way we move around it. We see a landscape that has been both developed and restored, where humans and nature can co-exist with a bit of effort from both sides. Again and again, habitat restoration has brought the Green Hairstreak butterflies (and many others) back from the brink of extinction.

### **A Vision for the Future**

The story of the Green Hairstreak butterfly is one of persistence and resilience. Should we continue to be as persistent in our efforts to conserve their habitat, the probability of their survival will increase. Despite the dramatic changes that have occurred over the past 250 years, there is still hope that we can coexist with the endemic species of this region, hope for a future in which delicate species such as the Green Hairstreak can thrive in the midst of our busy urban jungle -- where people stop to enjoy these stunning little creatures, take the time to get to know them, and see them as conscious beings, with agency, that deserve to live in a world that hears their story and works to protect them. Thanks to Nature in the City and the many stewards that work to restore the Green Hairstreak Corridor, we are already halfway there. If we take the time to see the world through the eyes of the butterfly, we can make a positive impact. The more we know about these butterflies and how they perceive and interact with the world around them, the better we can protect them in the years to come.

## Chapter 3: Plant-Butterfly Interactions

### Introduction

Plant-pollinator interactions form the basis of every ecosystem, yet around the globe, insects are declining at an alarming rate. Referred to by many as the “insect apocalypse” or an “ecological Armageddon,” these declines have been brought on by stressors such as urbanization and land-use changes, climate change, pollution, agriculture, etc., many of which co-occur (Wagner et al., 2021). These stressors have weakened the quality of plant-pollinator networks and reduced the services they provide (Burkle et al., 2013). Changes to insect communities can cause dramatic changes to entire ecosystem functioning, as insects provide valuable ecosystem services – most notably the pollination of 87% of all plant species and 75% of human-grown crops (Goulson, 2019). Because of this, plant-pollinator interactions are widely studied; Lepidoptera are the most studied of all insect orders (Wagner et al., 2021).

### Figure 20. Seaside Daisy Plant



*Figure 20 - Image of established Seaside daisy (Erigeron glaucus) plant at Baker Beach. (Photo Credit: Sarah Gomes)*

There are several flowering plants within the Green Hairstreak Corridor, such as Seaside daisy, Sea thrift, Beach strawberry, and Yarrow, that provide reliable nectar resources for the Green Hairstreak and other butterflies. The diverse range of nectar plants provides a well-balanced nutritious diet for butterflies, each plant species providing a different combination of the necessary vitamins and amino acids that support long-term survival and oviposition (Rani & Raju, 2016). Seaside daisies produce an abundance of bright purple and yellow flowers that are attractive to many pollinators (Fig. 20), and their frequent and consistent blooms provide a reliable nectar resource for butterflies throughout winter, spring, and summer.

There are several reasons why the Seaside daisy is well-suited for Green Hairstreak butterflies, in particular. Butterflies with a long proboscis are able to feed from a greater variety of nectar plants than those with a short proboscis and it is known that butterflies in the Lycaenidae family prefer flowers with small tubes (Rani & Raju, 2016). It follows that the Green Hairstreak's short proboscis limits the number of flowering plant species it is able to feed from, thus the short corolla tubes of the Seaside daisy are ideal. While short tubes generally do not produce a large amount of nectar, the center of a Seaside daisy flower contains a spiral of hundreds of individual disc flowers that each provide their own source of nectar, making a visit to one Seaside daisy flower an efficient use of a butterfly's time and energy.

Several floral traits influence pollinator visitation. Thompson (2001) studied visitation patterns between different insect types in response to floral display and floral design of Common yellow jasmine (*Jasminum fruticans*) in a generalist population system, finding that butterfly visits were positively correlated with the number of open flowers and flower size. Butterflies made more visits to plants with more open flowers and longer corolla lobes, and flower density

also proved to be important to all pollinator visitation. Lepidoptera (i.e., butterflies and moths) were the only insect types that showed a relationship with flower size, which they believe may be due to the positive correlation between flower size and nectar volume (Thompson, 2001). Similarly, Gómez et al. (2008) studied variation in pollinator visitation of different insect types based on floral traits of the wallflower, *Erysimum mediohispanicum*. Butterfly visitation was associated with highly rewarding plants that had a large number of flowers with large corolla diameters. They found that floral display was positively correlated with available nectar and pollen rewards, i.e., plants with a greater floral display were more attractive to pollinators (Gómez et al., 2008). Both Thompson (2001) and Gómez et al. (2008) included observations of all visiting butterflies within generalist population systems, which provide valuable foundational knowledge about plant-butterfly interactions, but they did not speak to the limitations of specialist species. Within the Green Hairstreak Corridor, it is unclear which floral traits influence Green Hairstreak preferences for Seaside daisy plants. Advancing our understanding of the species-specific interactions between butterflies and this reliable nectar plant will inform restoration decisions that aim to efficiently support Green Hairstreak butterfly populations in the future.

In this chapter we explore how Green Hairstreak butterflies interact with established Seaside daisy plants in restored urban habitats. We observed butterflies within the Green Hairstreak Corridor and monitored their interactions with Seaside daisy plants, supplemented by behavioral observations, to infer which plant and floral characteristics influenced their feeding habits. We hypothesized that butterflies would make more visits to Seaside daisies with the

greatest floral display and the largest flowers. Finally, we will use the information from this study to provide evidence-based recommendations for habitat management.

### **Methods**

We conducted an observational study during the Green Hairstreak's flight season of 2021 (March – May). We initially set out to monitor several restored habitat sites within the Green Hairstreak Corridor, including Grandview Park, Rocky Outcrop, Quintara Steps, and 12<sup>th</sup> & Pacheco. We visited each site to watch for Green Hairstreak butterflies for at least 1 to 2 hours, on multiple days, during ideal conditions (i.e., during peak pollinator activity on warm, sunny days). We spent a total of 14 days in the field, visiting restored habitats within the Green Hairstreak Corridor for 6 of those days; we spent one additional day scouting for Green Hairstreaks in the Presidio and Baker Beach area. While we observed multiple Green Hairstreak butterflies at Quintara Steps and one at Rocky Outcrop, we did not find them at any other sites. Therefore, we focused most of our observation efforts at Quintara Steps, where we recorded plant and flower characteristics of established Seaside daisy plants and plant-butterfly interactions.

## Study Area

**Figure 21. Quintara Steps**



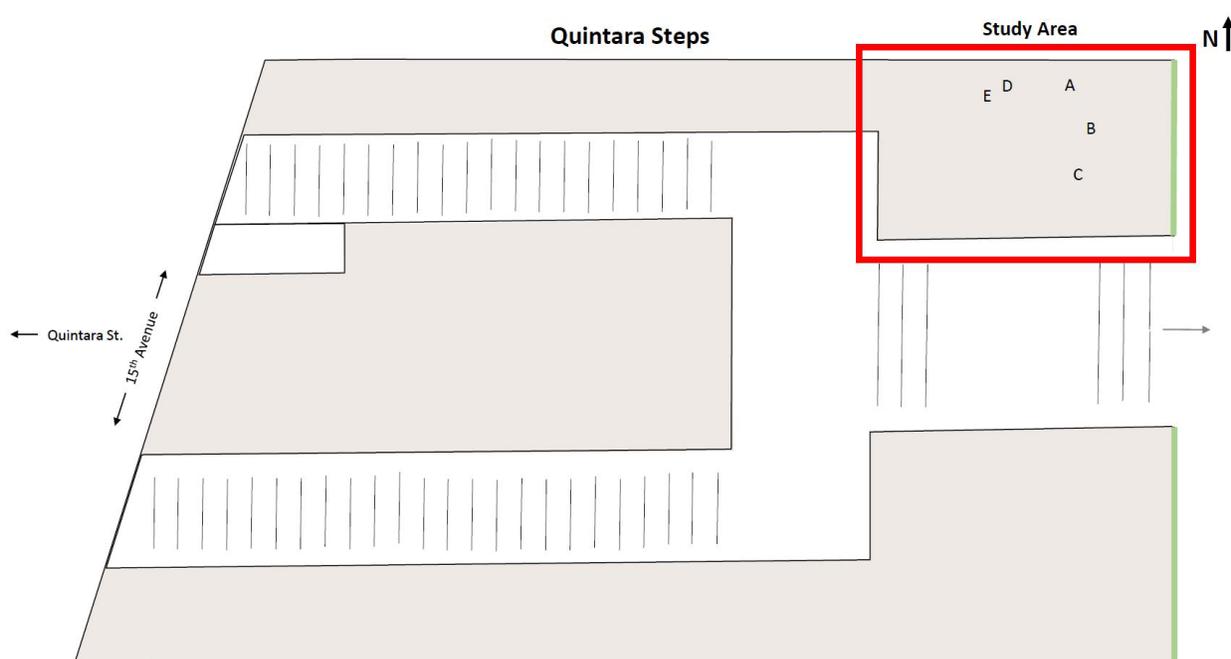
*Figure 21 - Image looking up toward (a) and looking out from (b) the upper level) of the restored habitat at Quintara Steps. (Photo Credits: Sarah Gomes)*

The Quintara Steps are located at the intersection of 15<sup>th</sup> Ave. and Quintara St. in the Inner Sunset District of San Francisco. Two levels of restored habitat wrap between and around staircases that extend up the hillside (Fig. 21a). This site is situated on a western-facing hillside, directly facing the Pacific Ocean, and is frequently inundated by dense coastal fog (Fig. 21b). This habitat ranges from 167 to 178 m in elevation, and with no buildings or other obstructions to the west, intercepts coastal fog as it moves up and over the hillside (Fig. 21b). During the butterfly's flight season, fog typically saturates the habitat in the morning hours and dissipates around 1100 hour, just before peak pollinator activity begins.

## Study Design

We arrived at Quintara Steps in the mornings at approximately 0900 hour to conduct plant measurements. We then observed butterfly visitation during peak butterfly activity from 1100 to 1400 hours. All butterfly observations were conducted on warm, sunny days with little wind, which are ideal conditions for butterfly flight.

**Figure 22. Quintara Steps – Site Diagram**

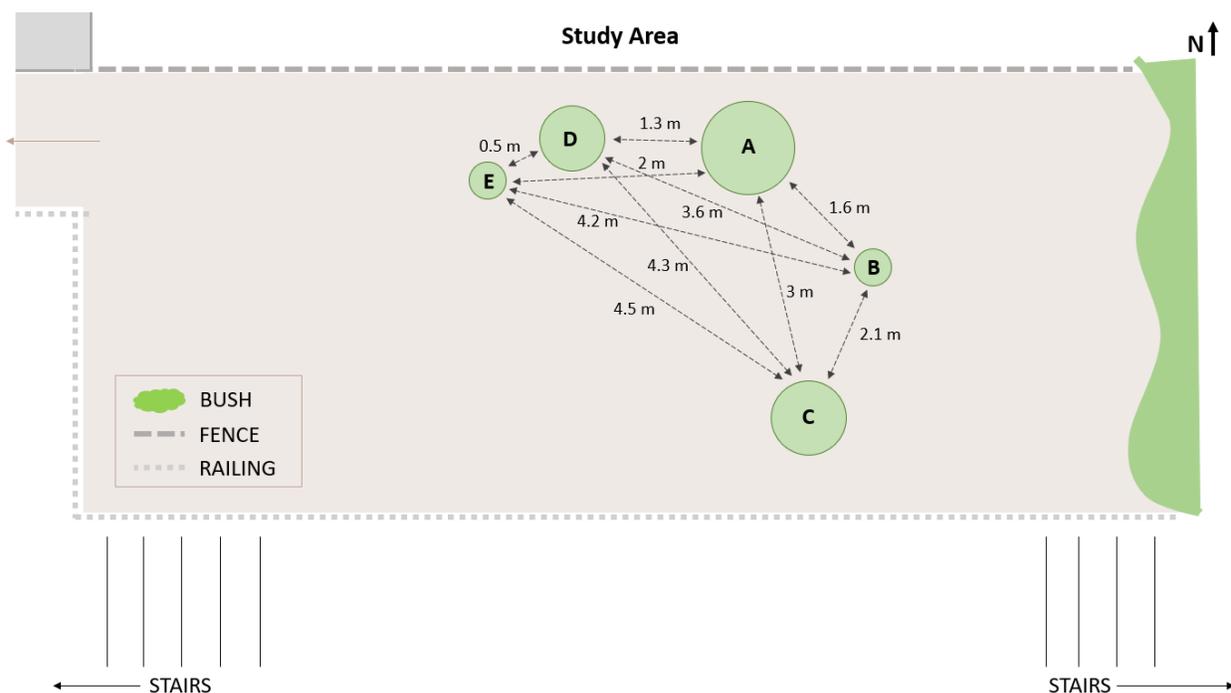


*Figure 22 - Diagram of Quintara Steps with outline of our selected study area (red) for butterfly observations. Light brown represents landscape with restored habitat. Letters A-E within Study Area represent Seaside daisy plants that were marked for observation.*

We chose to monitor plants in the northeastern level of habitat where butterflies were frequently found (Fig. 22). Within this study area, we monitored butterfly-plant interactions within a cluster of five established Seaside daisy plants within the same microclimate. Each plant differed in size and number of flowers; we observed one large, two medium, and two small

Seaside daisy plants for this study. We measured nearest neighbor distances between Seaside daisy plants to estimate foraging distances of butterflies (Fig. 23).

**Figure 23. Study Area Diagram**



*Figure 23 - Diagram of Study Area for butterfly observations on the northeastern portion of habitat at Quintara Steps. Circles represent Plants A - E that were marked for butterfly observations. Note: Diagram is a rough estimate and is not precise in scale.*

The northern boundary of the study area is a chain link fence with plastic slats, behind which is a neighboring backyard (Fig. 23). The western boundary of the study area is a railing, with a portion of habitat connecting to the lower level (Fig. 23). The eastern boundary of the study area is cut off by a large, dense bush that marks the end of the restored habitat (Fig. 23). This area is the highest portion of habitat, with an elevation of 178 m.a.s.l. (Google Earth). The stairs continue uphill past the bush, but the remaining landscape is primarily covered in ice plant and does not support Green Hairstreak butterflies. Lastly, the southern boundary is a railing that

divides the habitat from an area where people frequently walk or jog up and down the staircases (Fig. 23).

The butterflies typically stayed within the habitat boundaries, but occasionally flew over the neighboring fence – usually by accident. For example, butterflies would often fly straight up to mingle with mates and occasionally get blown into the neighboring backyard by large gusts of wind. Butterflies also occasionally flew across the southern landing to visit the opposing southeastern portion of habitat, but did not do so frequently.

**Figure 24. Study Plants**



*Figure 24 - Images of Study Area with circles and labels noting Plants A-E. (Photo Credits: Sarah Gomes)*

There were five Seaside daisies clustered within the center of the study area, and four others scattered throughout the study area. We marked the clustered plants that were located in the middle of the study area, which each varied in size and floral display, in order to understand which plant(s) the butterflies might prefer (Fig. 23 & 24).

### **Plant Measurements**

**Table 2. Definitions – Plant Characteristics**

*Table 2 - Definitions of plant and floral measurements used as proxies for nectar rewards available from Seaside daisy plants.*

Scale	Characteristics	Definitions
Canopy	Canopy Area	Approximate area (m <sup>2</sup> ), assuming a perfect circle ( $= \pi r^2$ )
	Number of Flowers	Total number of open composite flowers
	Number of Buds	Total number of buds and/or having no open disc flowers
	Flower Density	Number of open flowers per m <sup>2</sup> ( $= \text{Number of Flowers} / \text{Area}$ )
Flower	Composite Diameter	Diameter (mm) of composite flower
	Disc Diameter	Diameter (mm) of disc flowers
	Openness	Percentage of open disc flowers on each composite flower per plant
	Spent	Senescing disc flowers (i.e., flowers 100% open but turning brown)
	Damaged	Damaged ray and/or disc flowers (typically from insect herbivory)

At the start of the field season, we marked five established Seaside daisy plants (Plants A-E) with high-visibility marking ribbons to monitor for butterfly observations (Fig. 23 & 24). We quantified the following traits of each individual plant: canopy area, total number of flowers, and total number of buds (Table 2). We estimated the canopy area by measuring the diameter of the canopy of each plant at its longest two points and calculated the area under the assumption that the canopy was a perfect circle ( $A = \pi r^2$ ) (Table 2). We also calculated the flower canopy density by dividing the total number of open flowers by the plant area (m<sup>2</sup>) (Table 2).

**Figure 25. Daisy Flower Anatomy**

*Figure 25. Diagram of Seaside daisy flower anatomy, illustrating disc (yellow), ray (purple), and composite flowers. (Photo Credit: Sarah Gomes)*

We measured floral traits as proxies for nectar rewards afforded by each plant. Each composite flower contains hundreds of individual ray and disc flowers (Fig. 25); therefore, we were not able to directly measure the nectar volume and sugar concentration of each flower. Instead, we estimated the floral rewards per plant as a proxy for nectar availability. We used a digital caliper to measure the following traits of every composite flower with open disc flowers: flower size, central diameter, and percentage of open disc flowers (Table 2). We also made note of when flowers were spent and/or damaged, in the event that this might influence visitation (Table 2). We characterized flowers as “spent” if they had 100% open disc flowers that were starting to turn brown. We did not include flowers that had fully senesced and gone to seed in our floral measurements. In our analysis, we calculated average diameter of composite flowers

(mm), average diameter of disc flowers (mm), and average openness (%) of disc flowers per plant.

### **Butterfly Observations**

We made observations when butterflies are most active, between 1100 to 1400 hours. At the start of our field season, we observed butterfly behaviors and tried various observation methods; we determined that watching a cluster of plants of various sizes within the same microclimate was the best method to maximize efficiency and number of observations. We recorded butterfly behaviors near a cluster of plants toward the end of the Green Hairstreak's flight season, which we determined from the decline in butterfly sightings and field guide descriptions (Shapiro, 2007). Each time a butterfly landed on an individual Seaside daisy flower, we recorded the time (hh:mm), duration (sec), plant ID, and flower number of each visit. When possible, we made note of the percentage of open disc flowers on the visited flower after the butterflies had left. In our analysis, we calculated the total number of visits (defined as one visit to one flower) per plant, the total number of butterflies per plant, total duration (seconds) of visits per plant, average duration of visits, and the average number of butterflies per open flower on the plant. We documented visits from all butterfly species, although the majority of our observations were of Green Hairstreak butterflies. Of all 28 visits, only two visits were by another species – Umber Skipper butterflies (*Poanes melane*). By the end of our field season, we had two out of six days of successful sunny day butterfly observations (May 10 and 20, 2021) and one foggy day (May 11, 2021) to include in our results.

### **Results**

#### **Behaviors**

### Figure 26. Sunny vs Foggy Day Behaviors



*Figure 26 – Images of Coastal Green Hairstreak butterflies on a sunny day (a), feeding from a Seaside daisy flower, and on a foggy day (b), perched within a Coast buckwheat plant. (Photo Credits: Sarah Gomes)*

We observed that on sunny days Green Hairstreaks frequently perched on the tall stalks of Coast buckwheat and Dune tansy to bask in the sun. Flight was quick and sporadic; they often flew straight up when mates came near. Several butterflies, which we presumed to be males, appeared to wait for mates on tall stalks (Liam O’Brien, personal communication, July 19, 2019) and quickly took flight when other Green Hairstreaks approached. When mingling with mates high up in the air, butterflies occasionally got swept away by large gusts of wind, sometimes blowing over into the neighboring backyard or down to the lower level. They would often return to the study area to perch and/or feed. We found that most of the time spent feeding from nectar plants was from Seaside daisies (Fig. 26a). Upon closer observation, we found that when butterflies landed on the disc flowers of Seaside daisies, they often rotated in a circle as they ate (Fig. 26a). They would stretch their proboscis into each disc flower, then move to the adjacent

disc flower and rotate around until they were satisfied. To our surprise, they exhibited this feeding behavior on what we considered “spent” flowers, when the disc flowers had already begun to turn brown.

To understand the effect of coastal fog on Green Hairstreak behavior, we observed Green Hairstreaks on a cold, foggy day on May 11, 2021 (Fig. 26b). We found only one butterfly that day and observed that same butterfly for approximately 1 hour, recording each of its behaviors in our field notes. It stayed on the same Coast buckwheat plant for the entire hour (Fig. 26b), only moving around the plant in response to small changes in microclimate (i.e., wind or sun). As winds blew from the west, it nestled itself into the eastern side of the plant, where it stayed for most of the hour. As wind gusts increased, it moved further toward the base of the plant. Every time that the sun peeked out through breaks in the fog, the butterfly would quickly leave its sheltered location, moving up to the sunniest spot on the plant. Even during the very few, brief sunny moments, the butterfly did not take flight or visit other plants. When the sunlight vanished, the butterfly continued to nestle in its favored sheltered spot on the eastern side of the plant (Fig. 26b). As a passerby, it is common to see very little butterfly activity on foggy days. However, upon closer observation, we found that the butterfly was alert and ready to go, continuously moving itself to the best available microclimate within the plant.

### Figure 27. Territorial Checkerspot



Figure 27 - Image of territorial Variable Checkerspot butterfly (*Euphydras chalcedona*) perched on a blade of grass. (Photo Credit: Sarah Gomes)

We occasionally observed interactions with other butterfly species, including a male Variable Checkerspot (*Euphydras chalcedona*) butterfly that perched downhill from the marked Seaside daisies, above the corner of the western railing (Fig. 27). Variable Checkerspots can exhibit territorial behaviors, as it is known male butterflies will occasionally “defend small areas where they wait for receptive females to arrive or fly by” (Ehrlich & Hanski, 2004). We presume that this Checkerspot was displaying territorial behaviors, because it perched on a tall blade of grass (Fig. 27) and went after anything that flew by: butterflies, bees, and even birds that flew close to the ground. It did not visit any of the marked Seaside daisies, but it did chase Green Hairstreak butterflies occasionally and, although we did still observe feeding behaviors by Green Hairstreaks during that time, there is a chance that this may have influenced the other butterflies’ behaviors.

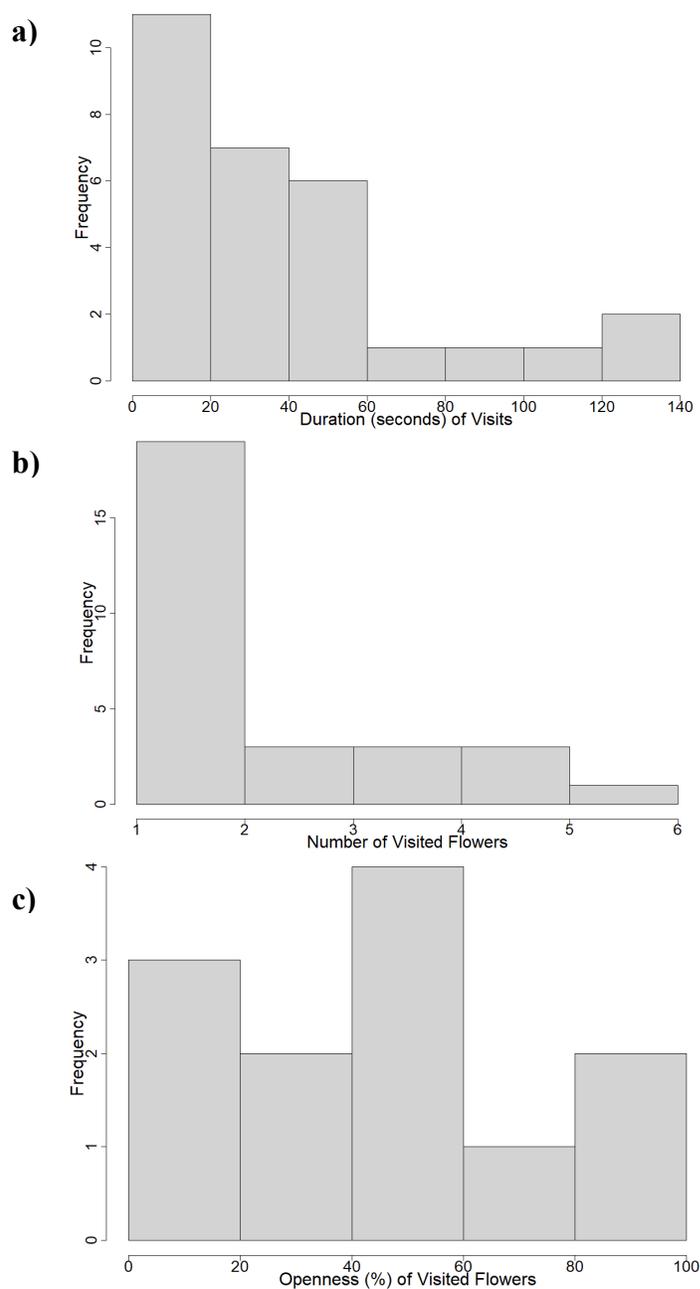
### Visitation

**Table 3. Visitation Statistics**

*Table 3 - Visitation statistics per plant (i.e., total number of flowers visited, total number of butterflies, total duration (sec) of all visits, average duration (sec) of individual visits, and average number of butterflies per open flower on a plant).*

Plant ID	Total Number of Flowers Visited	Total Number of Butterflies	Total Duration (sec) of Visits	Average Duration (sec) of Visits	Average Number of Butterflies per Flower
Plant A	25	9	995	39.8	0.05
Plant B	0	0	0	0	0
Plant C	1	1	13	13	0.02
Plant D	2	2	53	26.5	0.05
Plant E	1	1	77	77	0.10

Plant A received the most visits (a total of 25 visits made by nine butterflies) relative to the other seaside daisies we observed (Table 3). Plant D received two Green Hairstreak butterfly visits from two different butterflies. Plants C and E were each visited by only one Green Hairstreak. Plant B did not receive any visits during our observation period. Out of the 29 butterfly visits to seaside daisy plants, 93% were by Green Hairstreak butterflies and 7% were by UMBER Skipper butterflies (one visit each to Plants A & C). Butterflies spent the most time on Plant A, with a total of 995 seconds spent between all visits (Table 2). Visits to Plant A lasted from 0 to 130 seconds, with an average of 39.8 seconds per visit (Table 3). Although butterflies made more visits to Plant D than E, they spent more time on Plant E with a single visit of 77 seconds (Table 3). Butterflies spent a total of 53 seconds on Plant D, with an average of 26.5 seconds per visit (Table 3). The single visit to Plant C was short, lasting only 13 seconds (Table 3). Between all visits, butterflies frequently made short visits to individual flowers (Fig. 28a). Most visits lasted less than 20 seconds, with a similar frequency of visits between 20 – 60 seconds, and visits greater than 60 seconds were less common (Fig. 28a).

**Figure 28. Visitation Histogram**

*Figure 28 – Histograms of all visitation observations to Seaside daisy plants: a) duration (sec) of individual visits; b) number of flowers visited per butterfly; c) disc flower openness (%) of visited composite flowers.*

Most butterflies visited one or two flowers per plant before moving on to another plant or changing behavior (i.e., perching, flying, mating, etc.), and the greatest number of flowers visited

by a single butterfly was six flowers on one plant (Fig. 28b). We found that butterflies made more visits to composite flowers that had 50% or more open disc flowers (Fig. 28c). Similarly, butterflies spent 20% more total time on flowers that were 50% or more open compared to flowers that were less than 50% open (317 sec and 267 sec, respectively).

The number of visiting butterflies per open flower per plant was similar between plants, suggesting that flowers on each plant were similarly attractive to butterflies. Plant E had the highest average number of butterflies per open flower available on the plant (0.10) (Table 3). This was followed by Plants A and D, which both had an average of 0.05 butterflies per open flower (Table 3). Plant C had the lowest butterfly to open flower ratio (0.02) between the plants, although visitation rates were all similar (Table 3).

### Floral Rewards

**Table 4. Plant Characteristics**

*Table 4 - Comparisons between plant characteristics per plant for May 10<sup>th</sup>, 2021.*

Plant ID	Plant Size	Canopy Area (m <sup>2</sup> )	Flower Density	Number of Open Flowers	Number of Buds	Number of Damaged Flowers	Number of Spent Flowers	Average Diameter (mm) of Composite Flowers	Average Diameter (mm) of Disc Flowers	Average Openness (%) of Disc Flowers
A	Large	0.64	273	175	124	162	73	29.05	18.90	74.66
B	Small	0.13	346	45	15	31	28	26.69	15.71	79.78
C	Medium	0.5	192	96	58	59	15	26.11	17.96	41.72
D	Medium	0.38	100	38	35	0	18	19.16	19.16	81.58
E	Small	0.13	76	10	8	10	6	22.10	19.20	82.00

Plant A had the largest canopy area (Table 4) and was situated in an open space with its closest neighbor at 1.3 m distance (Fig. 23). Plant C was the second largest plant (Table 4) with a large Coast buckwheat plant directly adjacent to it (Fig. 24). It was also the closest plant to the railing that separates the walking path along the staircase (Fig. 23). Plant D was the third largest

plant (Table 4) with a large Coast buckwheat adjacent to it and was in close proximity to Plant E (Fig. 23 & 24), which was smaller in size (Table 4). Plant B was also a small plant (Table 4) and was close to another large Coast buckwheat (Fig. 24). In summary, the two closest plants in proximity to Plant A were Plants D and B, respectively. Plant D was a medium-sized plant, with the shortest distance from Plant A. Plant B was a small plant with less flowers, and had a greater distance from Plant A. Plant C was the second largest plant, but had the furthest distance from neighboring plants (Fig. 23).

Plant A had the greatest number of open flowers and the second highest flower density (i.e., number of flowers per m<sup>2</sup>) (Table 4). Of those flowers, 93% were damaged and 42% were spent (Table 4). Plant C had the second greatest number of open flowers, of which 69% were damaged and 16% were spent (Table 4). Despite its small size, Plant B had the highest flower density of all the study plants, and a greater number of open flowers than Plants D or E, of which 69% were damaged and 62% were spent (Table 4). Plant D had the second lowest canopy density and number of flowers, of which none were damaged and 47% were spent (Table 4). Lastly, Plant E had the lowest canopy density and lowest number of flowers, of which all were damaged and 60% were spent (Table 4).

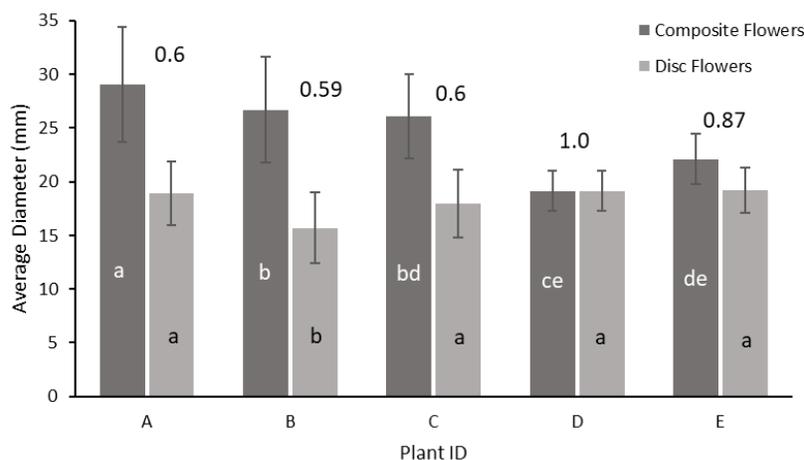
**Figure 29. Average Flower Size**

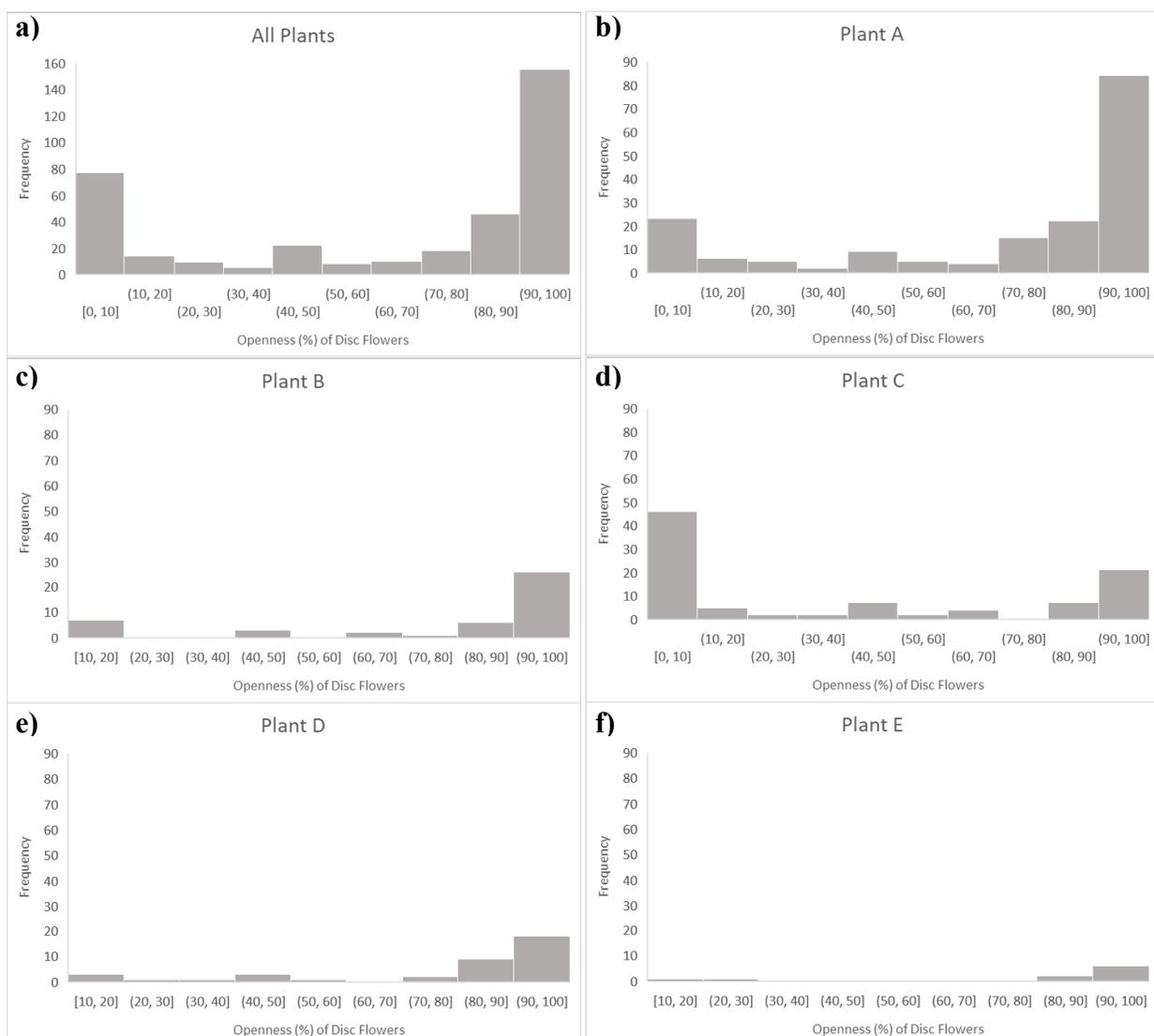
Figure 29 - Average diameter (mm) of composite flowers (dark grey) and disc flowers (light grey) per plant. Error bars represent standard deviation. Numerical values above bars represent the ratio between disc and composite flower size (i.e., disc:composite) per plant, where larger values indicate that the disc flowers are a greater proportion of the whole flower. Lowercase letters represent significant differences between plants ( $\alpha=0.05$ ), where white letters refer to composite flowers and black letters refer to disc flowers.

Across all plants, there appeared to be more variation in composite flower size than disc flower size, both within and between plants (Fig. 29); this is likely due to herbivory and damage of ray flowers. Plant A had the largest composite flowers, and this was significantly different from all other plants (Fig. 29). Flower size was followed by Plants B, C, E, and D, respectively (Table 4 & Fig. 29). Plant B had the second largest composite flowers, and was significantly different from all plants but Plant C ( $P = 0.96$ ). The size of composite flowers on Plant C was not statistically different from Plants B ( $P = 0.96$ ) and E ( $P = 0.07$ ). Plant D had the smallest composite flowers, but was not different than Plant E ( $P = 0.38$ ).

Plants E, D, and A had the largest average disc flowers, respectively, although they were each close in size (Table 4 & Fig. 29). Plant B had the smallest disc flowers and was significantly different from all other plants (Table 4 and Fig. 29). Disc flower size was not significantly different between any other plants.

Plant B had the highest size contrast (i.e., ratio between composite flower and disc flower size); Plant E had the lowest contrast (Fig. 29). There was no contrast between composite and disc flowers on Plant D (Fig. 29) because they had no remaining ray petals, which likely resulted from insect herbivory.

**Figure 30. Openness of Flowers**



*Figure 30 - Histograms of openness (%) of disc flowers per plant on May 10th, 2021.*

Plant A had the greatest total number of composite flowers, with greater openness of disc flowers (Fig. 30b). Histograms of flower openness show that most flowers on Plants A, B, D, and E were 70% or more open while Plant C mostly had 10% or less open flowers (Fig. 30d). On average, Plants E, D, and B, respectively, had the greatest average openness of disc flowers (Table 4). Plant C had considerably lower average openness than any of the other plants in our study (Table 4).

### **Discussion**

We observed a clear preference for Plant A by Green Hairstreak butterflies during our study period, which supported our hypothesis. Plant A received the greatest number of visits, by the greatest number of butterflies, as well as the longest time spent per plant (Table 3). These results are supplemented by our behavioral observations, in which butterflies that approached the cluster of Seaside daisies would either fly straight to Plant A, or hover over other marked plants and choose to feed from Plant A instead. There are a number of reasons why we believe the butterflies may have preferred Plant A over the other Seaside daisy plants we observed. Gómez et al. (2008) found a positive relationship between floral display and nectar rewards, meaning that plants with more flowers generally have more nectar available to pollinators. In our study, Plant A was the largest plant with greatest number of open flowers, which suggests that it also had the greatest nectar reward. In addition to this, most of the composite flowers on Plant A had disc flowers that were 70% or more open, which suggests that more nectar was readily available for visiting butterflies.

We found evidence to support our hypothesis that composite flower size would be an important explanatory factor of butterfly visitation to plants. In similar studies, Thompson (2001)

found that butterflies preferred flowers with longer corolla lobes and Gómez et al. (2008) found that butterflies preferred flowers with larger corolla diameters. In our study, butterflies frequently visited the plant with the largest composite flowers (Plant A), which was significantly larger than any other plant. Disc flower size did not significantly differ between plants, with the exception of Plant B. It is unclear whether butterflies are more attracted to ray or disc flower size based on the relevant literature, as the plants included in similar studies had different flower composition than Seaside daisies (Gómez et al., 2008; Thompson, 2001). On average, Plant B had the second largest composite flowers and E had the largest disc flower diameter (Table 4), but both received few if any visits from butterflies (Table 3). While we believe that flower size had some influence on visitation, it is possible that butterflies were first attracted to floral display and then considered overall flower size. However, the small number of visits we observed limited our inferential statistics, and we were unable to come to conclusions about the strength of the influence of flower size with the information provided.

While butterflies did visit the plant with the greatest floral display and largest flowers most frequently, we do not believe these were the only determinants of foraging behavior. Of the other plant and floral traits we studied, we believe openness and location also influenced feeding preferences. We found that butterflies made more visits to flowers that were 50% or more open (Fig. 28c); of the plants that butterflies spent the most time at (Plants A, E, and D, respectively), majority of disc flowers were 70% or more open, which we believe equates to more available nectar based on relevant literature (Gómez et al., 2008). Further, butterflies spent the most time on Plant A, which had the greatest frequency of flowers that were greater than 70% open (Fig.

30b), and spent the least time on Plant C, of which most flowers were less than 20% open (Fig. 30d).

It appears that visits to other marked plants were determined by their proximity to Plant A. Its two nearest neighbors, Plants D and B (Fig. 23), received two and zero visits, respectively (Table 3). Given the choice between Plant D or B, it follows that it would be more energy-efficient for butterflies to choose Plant D because of the shorter distance and greater floral rewards. Similarly, Plant B had greater canopy density and more open composite flowers than Plant E of the same size, yet Plant E received one long visit (Table 3) which may be from its close proximity to Plant D (Fig. 23). Plant C received the least attention, which we believe is due to the longest distance to Plant A, as well as its close proximity to the walkway (Fig. 23) and its limited openness (Fig. 30d). Following the same theory as above, it is not time and energy-efficient for a butterfly to travel a greater distance to a plant with less nectar readily available, when there are better choices (e.g., Plant A) available nearby. From the eyes of a butterfly, it makes sense that they would choose to feed from plants with the greatest potential reward while expending the least amount of time and energy.

### **Restoration Recommendations**

The outcome of this research advances our basic understanding of how a specialist butterfly uses restored habitat in an urban landscape. We show that when given a choice, Green Hairstreak butterflies visit nectar plants with the greatest floral display (i.e., the greatest number of flowers) most often, and this is likely associated with greater nectar rewards. Given that butterflies prefer larger plants with many flowers, we recommend that managers, site stewards, and neighbors focus on maintaining large plants or create a large cluster from several smaller

plants. Large plants would also reduce wind speed in the lower 1 to 2 m, providing shelter for butterflies during unideal weather conditions.

Studies have shown that drought stress can negatively impact the number of floral rewards available to pollinators (Carroll et al., 2001). Our previous work has shown that fog alone can help to alleviate the negative effects of soil water deficit on the photosynthesis rates of Seaside daisy plants (Gomes & Baguskas, in press). Therefore, planting Seaside daisy plants in restored habitat where coastal fog exposure is maximized, i.e., at higher elevations where fog is intercepted, could improve the long-term survival of Seaside daisy plants in critical Green Hairstreak habitats. These habitat restoration recommendations that aim to alleviate plant water stress may also improve the floral rewards available to adult butterflies (Carroll et al., 2001).

Proximity to large plants seemed to influence visits to smaller plants in our study; therefore, we recommend that restoration managers, site stewards, and neighbors cluster nectar plants, when possible, to limit foraging distance between plants. This will likely improve visits to smaller plants and increase the efficiency of butterfly foraging, as similar studies have shown that clustering improves pollinator visitation (Akter et al., 2017). While the Seaside daisy is a reliable nectar resource for the Green Hairstreak butterfly, butterflies also benefit nutritionally from feeding on a diverse range of nectar plants (Rani & Raju, 2016); therefore, managers and site stewards should consider nectar plant diversity and nearest neighbors when planning a restoration site. This study provides foundational knowledge of the interactions between Green Hairstreak butterflies and Seaside daisy plants; restored habitats would benefit from more analysis of the interactions between butterflies and different plant species in the future.

## Conclusion

When presented with a cluster of Seaside daisies, Green Hairstreak butterflies tended to visit the plant with the greatest floral display and largest flowers. Plant size, location, number of open flowers, composite flower size, and openness of disc flowers were the best predictors of butterfly visitation. Flower size did not appear to impact visitation in our study as we had initially hypothesized. Butterflies visited and spent considerably more time on Plant A than on any other plant we observed. This pattern is likely attributed to Plant A's large canopy area, greatest number of open flowers (most of which were 70% open or more), large composite flowers, and location in an open space that was not obstructed from view by neighboring plants. We believe visits to smaller plants were determined by proximity to Plant A and floral display. In other words, butterflies chose to visit plants that had the greatest potential reward while exerting the least amount of energy. This information can be used to inform restoration efforts, as outlined in our study: we recommend that management promote plant growth and floral rewards, as well as cluster nectar plants to maximize the efficiency of butterfly movements.

## Chapter 4: Plant Physiology

### Introduction

From tropical forests to deserts, fog plays a crucial role in the functioning of ecosystems around the world (Weathers et al., 2019). It supports plants in a myriad of ways, such as augmenting plant water availability (Baguskas et al., 2016; Dawson, 1998; Fischer et al., 2016; Vasey et al., 2012), buffering heat stress (Oliphant et al., 2021) and transporting nutrients (Weathers et al., 2019). Studies have shown that fog becomes an even more vital resource in areas where water is limited, such as in arid and semi-arid ecosystems (Fischer et al., 2009, Weathers et al., 2019). There are three primary mechanisms by which fog can alleviate plant water stress: 1) lower temperatures and higher relative humidity reduces evapotranspiration rates (Baguskas et al. 2021; Burgess & Dawson, 2004; Chung et al. 2017; Fischer et al., 2009), 2) fog drip from the plant canopy to the soil can increase water availability (Baguskas et al. 2016; Ewing et al., 2009; Fischer et al., 2016), and 3) direct uptake of fog water by the leaves (Baguskas et al., 2016; Burgess and Dawson, 2004; Eller et al., 2013; Gotsch et al., 2014; Limm et al., 2009). Fog drip is largely influenced by canopy structure (Ewing et al., 2009; Vasey et al., 2012; Weathers et al., 2019). For example, Ewing et al. (2009) studied plants' physiological responses to water fluxes in a California redwood forest and found that, during fog season, below-canopy water fluxes were greatest at the forest edge; tree physiology also mirrored this pattern, where water stress was lower at the forest edge and greater in the interior forest. Many plants in foggy areas also have the capacity to absorb water directly through their leaves (Burgess and Dawson, 2004; Limm et al., 2009). Limm et al. (2009) found that 80% of the plant species they studied in the redwood forest (i.e., canopy trees, shrubs, understory ferns, etc.)

relied on foliar uptake to hydrate leaves. Vasey et al. (2012) studied dry-season water potential ( $\Psi_{\min}$ ) along a coast-to-interior fog gradient in chaparral shrubs of Central California and found that maritime chaparral regions had less negative  $\Psi_{\min}$  (i.e., higher water status) than interior chaparral regions, which was attributed to greater water availability from the summertime marine layer (Vasey et al., 2012). The relatively low canopy height of such regions likely increases fog drip to the soil, while providing sufficient leaf wetting to support foliar uptake (Vasey et al., 2012).

Fog frequently inundates the California coastline during summer months (June-August), alleviating plants' water and heat stress during an otherwise warm and dry period. The climatic benefits of fog (i.e., increased diffuse light, decreased vapor pressure deficit, increased water availability, etc.) can increase water-use and light-use efficiency of plants, which increases photosynthesis rates and overall plant survival. In fog-adapted ecosystems, the importance of coastal fog in supporting plant function during summertime also has implications for other species that depend on those plants, such as pollinators. For example, studies have shown that drought stress can negatively impact floral resources available to pollinators and therefore influence plant-pollinator interactions (Carroll et al., 2001; Burkle and Runyon, 2016). By alleviating water stress and improving plant survival, fog also has the potential to influence the amount of nectar resources available to pollinators. However, the links between fog, nectar plants, and pollinators have not yet been studied.

The Coastal Green Hairstreak relies on coastal sand dune habitat in areas that are frequently covered with fog. Butterfly distribution within the Green Hairstreak Corridor is patchy and Green Hairstreak populations consistently favor three of these habitats. While the

reasons butterflies favor these sites are unclear, all three inhabited sites are west-facing to the Pacific Ocean and are among the first habitats to intercept dense coastal fog advecting onshore. Additionally, each site varies in degree of stewardship and irrigation. A limitation to successful habitat restoration in the Green Hairstreak Corridor is the ability to provide the plants with water through irrigation. The relative importance of fog and irrigation in supporting plant function in fog inundated habitats remains unclear. Investigating the physiological mechanisms that drive plant-butterfly interactions is an important first step in developing a resilient ecosystem.

### Figure 31. Seaside Daisies Capturing Fog



*Figure 31 - Seaside daisies capture coastal fog droplets on the leaf surface and hairs of buds, leaves, and flower stems in restored butterfly habitat, Quintara Steps. (Photo Credits: Sarah Gomes)*

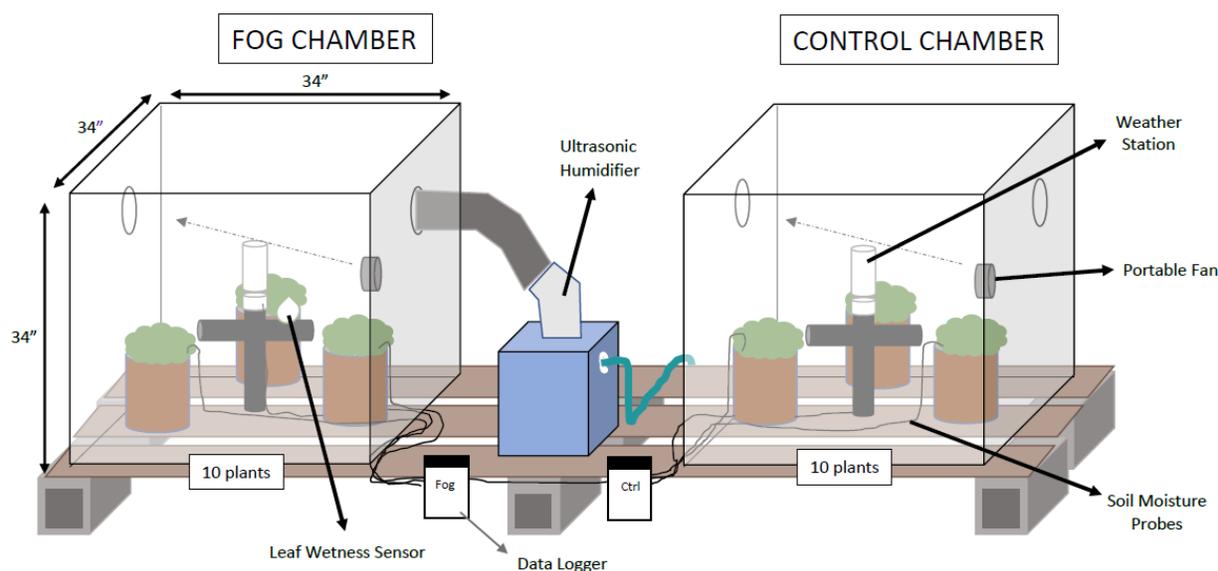
Fog is a crucial component of the coastal sand dune habitat where Green Hairstreak butterflies reside, frequently saturating the plants that this butterfly relies on (Fig. 31). It is likely that the butterfly's host and nectar plants rely heavily on fog to provide water to support photosynthesis during the dry months that typically occur during the butterfly's flight season.

The Seaside daisy is one of the primary nectar resources for the Coastal Green Hairstreak butterfly, and the impacts of fog on Seaside daisy functioning has not been studied previously. In this chapter we conducted a manipulative fog experiment to address the research question: How do coastal fog and irrigation impact the physiological function of Seaside daisies? We hypothesized that coastal fog enhances the leaf-level physiological function (namely photosynthesis rates) of Seaside daisy plants, especially for those that do not experience regular irrigation.

## Methods

### Chamber Structure

**Figure 32. Chamber Structure**



*Figure 32 - Diagram of chamber structure and instruments used in controlled fog experiment.*

Seaside daisy plants were placed inside of two plastic chambers, a “Fog Chamber” and a “Control Chamber” (Fig. 32). Both chambers were elevated from the ground and placed on a platform made of wooden planks and cinderblocks. Spacing between the wooden planks (~ 5 cm

allowed for some air flow in and out of the chambers. Chambers were constructed with a PVC pipe frame (86 cm x 86 cm x 86 cm), with fitted plastic sheets covering all sides, except for the bottom. Two holes were cut into the opposing side walls to allow some air flow through the chamber. A semi-rigid aluminum duct attached an ultrasonic humidifier (Model MBH12, Mainland Mart Corp.) to the Fog Chamber through one of the chamber's side holes. The ultrasonic humidifier we used produces fog droplets around 10 microns in diameter (Baguskas et al. 2016). We installed a fan inside each chamber to ensure that wind speed was similar in both chambers. Four-speed, 360° desk fans were clipped onto the left inside wall of each chamber, pointing diagonally, to promote mixing. The Control Chamber fan was set to maximum speed 4. The Fog Chamber fan was set to speed 2, to account for the added wind speed from the fog machine.

### **Environmental Conditions**

We installed an all-in-one micrometeorological sensor (ATMOS 41, Meter Group Inc.) in the middle of each chamber to monitor microclimate conditions during simulated fog events (Fig. 1). We monitored solar radiation ( $\text{W m}^{-2}$ ), precipitation (mm), wind speed ( $\text{m s}^{-1}$ ), air temperature ( $^{\circ}\text{C}$ ), vapor pressure (kPa), and vapor pressure deficit (VPD, kPa). In addition, we installed one leaf wetness sensor (PHYTOS 31, Meter Group Inc.) in the Fog Chamber to monitor leaf wetness during fog events (Fig. 32).

Volumetric soil moisture probes (EC-5, Meter Group Inc.) were inserted, vertically from the soil surface (~5 cm depth), into two plants per treatment group to measure volumetric soil water content ( $\text{m}^3 \text{m}^{-3}$ ) (Fig. 32). This placement allowed us to detect any small changes in

shallow soil moisture that might occur from fog drip. Microclimate and soil moisture observations were recorded every 15 minutes.

## Experimental Design

**Table 5. Treatment Groups**

*Table 5 - Fog and irrigation treatment groups used in controlled fog experiment (n=5 plants per treatment group, N=20 plants total).*

<b>Treatment Groups</b>	<i>Fog</i>	<i>No Fog</i>
<i>Irrigation</i>	Fog + Irrigation (Fog + Irr)	Irrigation Only (Irr)
<i>No Irrigation</i>	Fog Only (Fog)	Control (Ctrl)

We exposed plants to varied levels of fog and irrigation, then measured leaf-level physiological responses. Seaside daisy plants (N=20) were randomly separated into the following four treatment groups (n=5 per treatment group): Fog and Irrigation (Fog + Irr), Fog Only (Fog), Irrigation Only (Irr), and Control (Ctrl) which received neither fog nor irrigation (Table 5). This experiment was conducted entirely outdoors. Seaside daisy plants were grown under ambient conditions and were only placed within plastic chambers during morning treatment events.

Simulated fog treatments were administered for three consecutive days per week, for six weeks, between mid-February and March, 2021. Simulated fog events began in the morning, just before sunrise, from 0700 to 0900 hours. We chose two hours in the morning because this is typically when fog is prevalent. We limited our simulation to a two-hour duration because fog generated by the ultrasonic humidifier sufficiently immersed plant canopies within that time. Plastic covers were placed over the PVC frames 15 minutes prior to the official start time (0645 hour). This allowed fog to fully saturate the Fog Chamber by the start of the 2-hour treatment events. Plastic covers were taken off immediately after each event (0900 hour) so that plants had

time to dry off before measuring leaf gas-exchange rates. Both chambers followed the same procedure, the only difference being that the Control Chamber did not experience fog.

All plants received some additional water to ensure that they stayed alive for the duration of the experiment. However, irrigated plants received more consistent water than the non-irrigated plants. Irrigated plants (Fog+Irr and Irr) each received 1 liter of water on the night before the start of each treatment week. During heat waves when soil dried rapidly, irrigated plants also received an additional 1 liter of water at the end of the week to keep soil moist. Non-irrigated plants (Fog and Ctrl) only received water when the soil was so dry that plants began to wilt. Even so, non-irrigated plants were only watered at the end of each treatment week i.e., soil moisture was at its lowest point during the experiment before hydrating plants.

### **Physiological Measurements**

Following simulated fog events, plants were placed in the sun for approximately one hour to allow leaves to fully dry before measuring leaf physiology. We used a portable photosynthesis system (Model Li-6800, LI-COR Biosciences) to measure leaf-gas exchange rates through non-destructive survey measurements. Plant survey measurements were collected on sunny, warm days. In total, we sampled all 20 plants (n=5 per treatment group) on 6 separate days during the study period. Each day, two leaves per plant were sampled from each plant between mid-morning to early afternoon (1000 – 1300 hours), following the simulated fog events.

All leaf gas-exchange measurements were taken with a 2 cm<sup>2</sup> aperture in the leaf chamber. Constant settings included pump flow (500  $\mu\text{mol s}^{-1}$ ), chamber pressure ( $\Delta P_{\text{cham}}=0.1$  kPa), carbon dioxide concentration within the sample analyzer ( $\text{CO}_2\_s = 400 \mu\text{mol m}^{-1}$ ), fan speed (10,000 rpm), geometry (broad leaf), and oxygen (21%).

Due to fluctuating cloud patterns during measurement hours, we chose to control light levels in the leaf chamber. Prior to the experiment, we conducted a series of light response curves from four different Seaside daisy plants to find the light saturation point where maximum photosynthesis occurred. While each plant varied slightly, maximum photosynthesis generally occurred around  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Therefore, we adjusted fluorometer settings for light levels within the leaf chamber ( $Q_{\text{in}}$ ) to maintain  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  for plant survey measurements. It is important to note that light levels of  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  would not occur under natural foggy conditions. The purpose of this setting is to remove the effect of diffuse light and isolate other microclimatic benefits, such as temperature, humidity, and water availability.

Leaf temperature ( $T_{\text{leaf}}$ ) and relative humidity ( $\text{RH}_{\text{air}}$ ) were allowed to vary based on outside conditions. Leaf temperature ( $T_{\text{leaf}}$ ) ranged from 18-21 °C. Relative humidity of the air within the leaf chamber ( $\text{RH}_{\text{air}}$ ) ranged from 50-70%.

### **Statistical Analysis**

We calculated the average physiological response (photosynthesis rates and stomatal conductance) of the two leaves we sampled per plant. We pooled the physiological observations across the 6 sampling days because we found no significant differences in physiological responses between sampling dates. We performed an analysis of variance (ANOVA) to test for differences in physiological responses between treatment groups. We tested for an interaction between fog and irrigation treatments with respect to photosynthesis and stomatal conductance. When the ANOVA was significant ( $P < 0.05$ ), we performed a post-hoc Tukey HSD test to identify the treatment groups that differed significantly from one another. Statistical analyses were performed using 'aov' and 'Tukey HSD' functions in the 'stats' package in RStudio version

1.0.143. We tested for a normal distribution in the data using the Shapiro-Wilk's test, and found that data met normality assumptions.

Micrometeorological observations were recorded every 15 minutes from each sensor and then aggregated by averaging over the two hours of each chamber experiment. We then calculated the average conditions in the Fog and Control Chambers of all six sampling days. We calculated the average volumetric soil moisture (5 cm) of both plants per treatment group. An ANOVA and post-hoc Tukey HSD test were performed to identify significant differences between treatment groups for both micrometeorological and soil moisture observations.

We used a least-squares regression analysis to test for relationships between leaf-level photosynthesis and environmental factors (ambient temperature, VPD, soil moisture) within each treatment group. Explanatory factors were not auto-correlated. This statistical analysis was performed using the 'lm' statistical package in RStudio version 1.0.143.

## Results

**Table 6. Leaf-Gas Exchange Rates and Microclimate Variables**

*Table 6 - Average photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ), soil moisture ( $\text{m}^3 \text{m}^{-3}$ ), vapor pressure deficit (kPa), and ambient temperature ( $^{\circ}\text{C}$ ) per treatment group.*

Treatment Groups	Photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Stomatal Conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ )	Soil Moisture ( $\text{m}^3 \text{m}^{-3}$ )	Vapor Pressure Deficit (kPa)	Ambient Temperature ( $^{\circ}\text{C}$ )
Fog + Irrigation	$13.08 \pm 3.01$	$0.15 \pm 0.15$	$0.25 \pm 0.04$	$0.15 \pm 0.14$	$8.64 \pm 1.85$
Fog Only	$12.11 \pm 2.63$	$0.13 \pm 0.13$	$0.07 \pm 0.02$	$0.15 \pm 0.14$	$8.64 \pm 1.85$
Irrigation Only	$10.39 \pm 3.01$	$0.11 \pm 0.11$	$0.25 \pm 0.02$	$0.26 \pm 0.19$	$7.45 \pm 0.72$
Control	$9.24 \pm 2.21$	$0.09 \pm 0.09$	$0.05 \pm 0.02$	$0.26 \pm 0.19$	$7.45 \pm 0.72$

**Table 7. ANOVA Tukey HSD Test Results**

Table 7 - ANOVA Tukey HSD test results comparing the actual difference (diff.) and significance value (p-value) of photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ), soil moisture ( $\text{m}^3 \text{m}^{-3}$ ), and ambient temperature ( $^{\circ}\text{C}$ ) between treatment groups.

Treatment Groups	Photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )		Stomatal Conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ )		Soil Moisture ( $\text{m}^3 \text{m}^{-3}$ )		Ambient Temperature ( $^{\circ}\text{C}$ )	
	diff.	p-value	diff.	p-value	diff.	p-value	diff.	p-value
Fog vs Ctrl	2.87	<b>0.00</b>	0.05	<b>0.00</b>	0.01	<b>0.03</b>	1.19	<b>0.00</b>
Fog+Irr vs Ctrl	3.84	<b>0.00</b>	0.06	<b>0.00</b>	0.20	<b>0.00</b>	1.19	<b>0.00</b>
Irr vs Ctrl	1.15	0.45	0.02	0.53	0.20	<b>0.00</b>	-2.66	1.00
Fog+Irr vs Fog	0.97	0.52	0.02	0.52	0.18	<b>0.00</b>	0.00	1.00
Irr vs Fog	-1.72	0.10	-0.03	0.23	0.18	<b>0.00</b>	-1.19	<b>0.00</b>
Irr vs Fog+Irr	-2.69	<b>0.00</b>	-0.04	<b>0.01</b>	0.00	1.00	-1.19	<b>0.00</b>

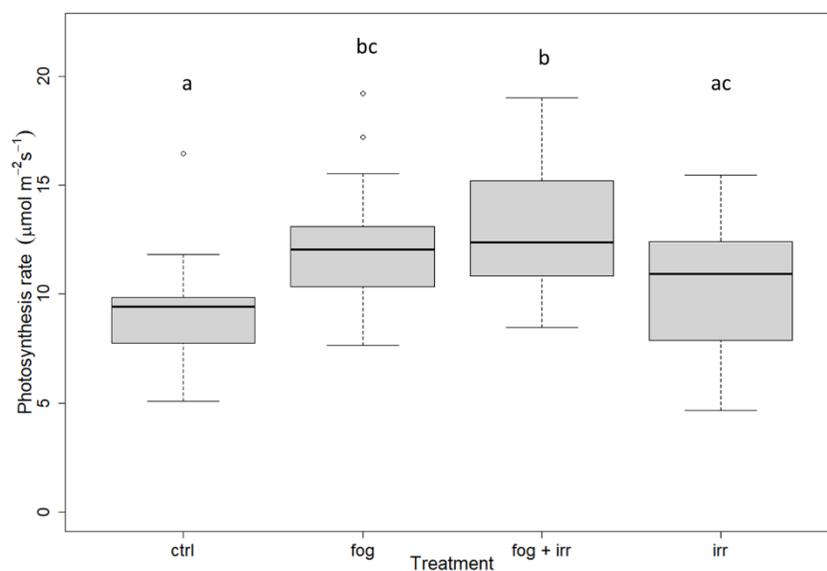
**Figure 33. Photosynthesis Rates**

Figure 33 - Boxplot of maximum photosynthesis rates ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), for  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR, per treatment group, following 2-hour simulated morning fog events. Solid black line represents average, box edges represent 25th and 75th percentiles, whiskers represent minimums and maximums, and circles represent outliers. Letters above boxplots represent significant differences between groups ( $\alpha = 0.05$ ). Results from Tukey HSD test are shown in Table 7.

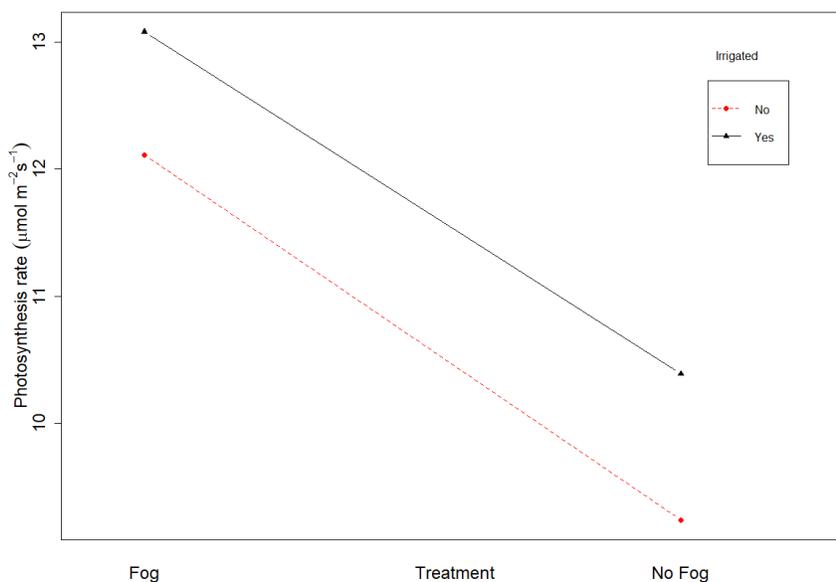
**Figure 34. Interaction Plot – Fog & Irrigation**

Figure 34 - Interaction plot between fog and irrigation treatments with respect to photosynthesis ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

In both the irrigated and non-irrigated groups, plants that received fog had higher average maximum photosynthesis rates (A) than plants that did not receive fog (Table 6 & Fig. 33). For plants that received fog, this increase in photosynthesis was greater in non-irrigated plants than in irrigated plants; non-irrigated plants increased by 31% ( $\Delta A_{(\text{Fog})-(\text{Ctrl})} = 2.87 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and irrigated plants increased by 26% ( $\Delta A_{(\text{Fog}+\text{Irr})-(\text{Irr})} = 2.69 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). In other words, fog-boosted photosynthesis became more important when soil moisture was low. Differences in photosynthesis between treatment groups were significant ( $P < 0.05$ ) except between Fog + Irr versus Fog ( $P = 0.52$ ), Irr versus Ctrl ( $P = 0.45$ ), and between Fog versus Irr ( $P = 0.10$ ) (Table 7). This lack of difference suggests that plants within the same chamber functioned similarly. Treatment, temperature, and soil moisture were highly significant explanatory factors and explained 46% of variation in photosynthesis ( $R^2 = 0.46$ ). VPD was marginally significant, but

likely also influenced photosynthesis. There were no significant interactions between fog and irrigation treatments that influenced photosynthesis (Fig. 34).

**Figure 35. Stomatal Conductance**

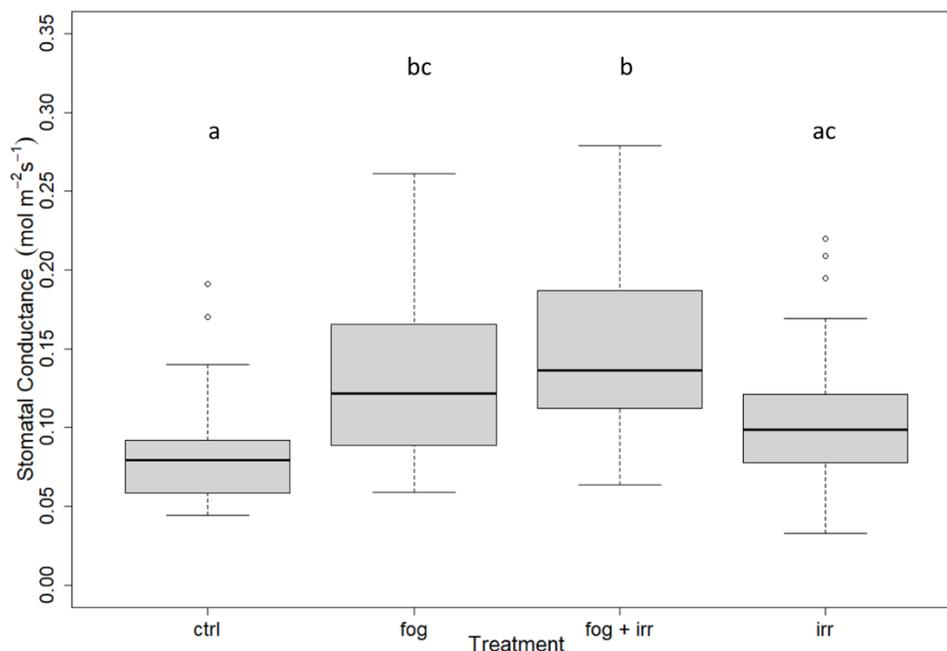


Figure 35 - Boxplot of stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ) per treatment group, following 2-hour simulated morning fog events. Solid black line represents average, box edges represent 25th and 75th percentiles, whiskers represent minimums and maximums, and circles represent outliers. Letters above boxplots represent significant differences between groups ( $\alpha = 0.05$ ). Results from TukeyHSD test are shown in Table 7.

Similarly, plants that received fog had higher average stomatal conductance ( $g_s$ ), regardless of irrigation (Table 6 and Fig. 35). This increase in stomatal conductance was greater in non-irrigated plants compared to irrigated plants: non-irrigated plants increased by 52.5% ( $\Delta g_s$  (Fog)-(Ctrl) =  $0.05 \text{ mol m}^{-2} \text{ s}^{-1}$ ) and irrigated plants increased by 41.5% ( $\Delta g_s$  (Fog+Irr)-(Irr) =  $0.04 \text{ mol m}^{-2} \text{ s}^{-1}$ ), suggesting that added fog was more important to stomatal conductance when soil moisture was low. Differences in  $g_s$  among treatments were significant, with the exception of Fog + Irr versus Fog ( $P=0.52$ ), Irr versus Ctrl ( $P=0.53$ ), and Fog versus Irr ( $P=0.23$ ) (Table 7), again suggesting that plants within the same chamber functioned similarly. This information further

suggests that plant function was influenced by both soil moisture and microclimate conditions: treatment, soil moisture, and temperature were significant in explaining 23% of variation in stomatal conductance ( $R^2 = 0.23$ ). VPD was moderately significant but likely also influenced stomatal conductance. There were no significant interactions between fog and irrigation that influenced stomatal conductance.

**Figure 36. Soil Moisture**

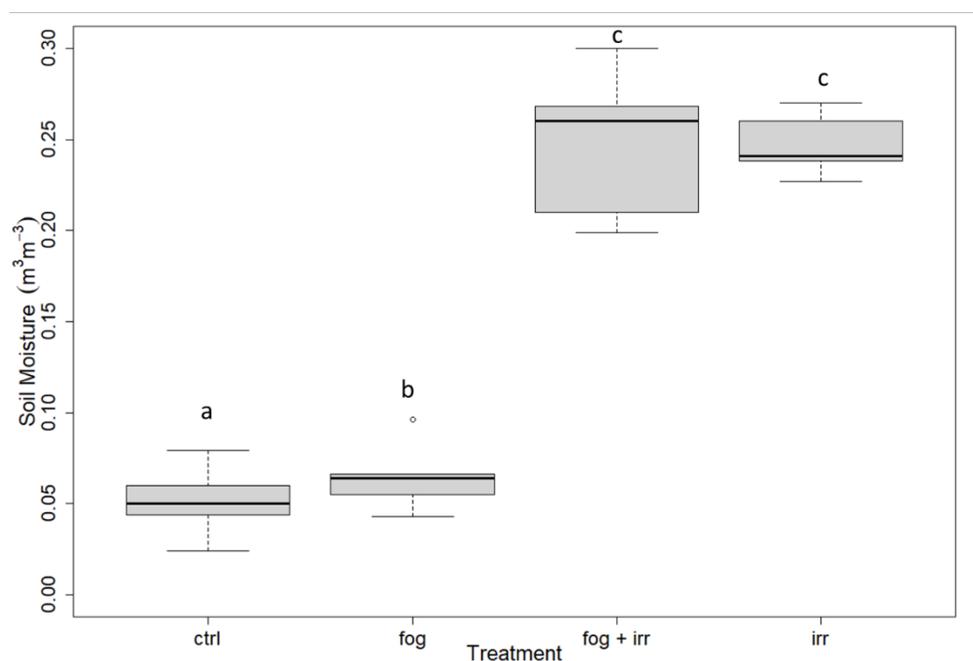


Figure 36 - Boxplot of soil moisture ( $m^3 m^{-3}$ ) per treatment group, measured as combined averages during 2-hour simulated fog events. Solid black line represents average, box edges represent 25th and 75th percentiles, whiskers represent minimums and maximums, and circles represent outliers. Letters above boxplots represent significant differences between groups ( $\alpha = 0.05$ ). Results from TukeyHSD test are shown in Table 7.

Average soil moisture (SM) was similarly high between the irrigated plants and similarly low between non-irrigated plants (Table 6 & Fig. 36). Soil moisture differed significantly between treatment groups, with the exception of Fog + Irr versus Irr ( $P = 0.99$ ) (Table 7). However, while there was a significant difference in soil moisture between the Fog versus Ctrl groups ( $P = 0.03$ ), the actual difference was negligible ( $SM_{Fog-Ctrl} = 0.01 m^3 m^{-3}$ ) (Table 7).

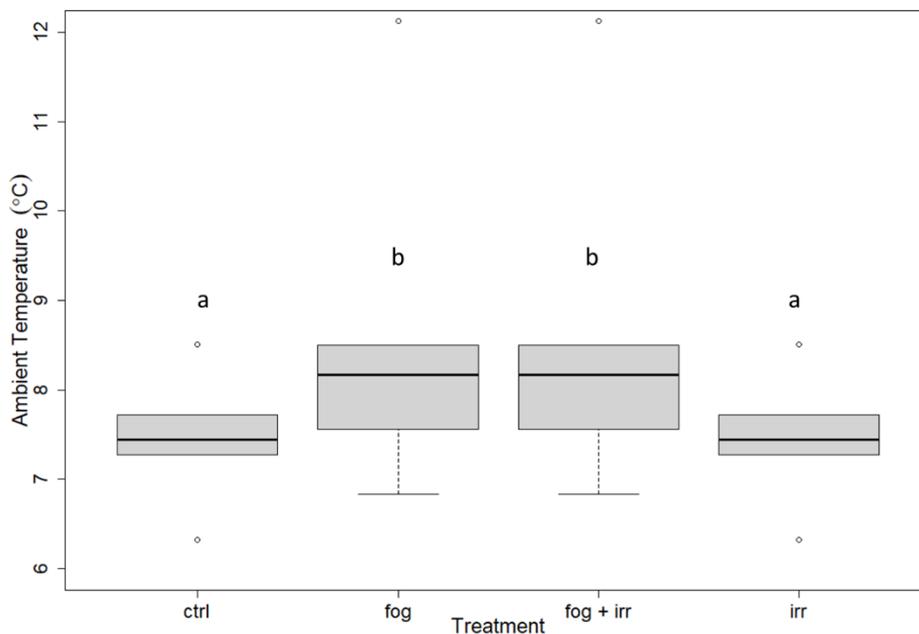
**Figure 37. Ambient Temperature**

Figure 37 - Boxplot of ambient temperature ( $^{\circ}\text{C}$ ) per treatment group, measured as combined averages during 2-hour simulated fog events. Solid black line represents average, box edges represent 25th and 75th percentiles, whiskers represent minimums and maximums, and circles represent outliers. Letters above boxplots represent significant differences between groups ( $\alpha = 0.05$ ). Results from TukeyHSD test are shown in Table 7.

Mean ambient temperature was  $1.2\text{ }^{\circ}\text{C}$  warmer in the Fog Chamber ( $8.6\text{ }^{\circ}\text{C}$ ) than in the Control Chamber ( $7.5\text{ }^{\circ}\text{C}$ ), and this difference was statistically significant (Table 6 & Fig. 37). This increase was unlike natural conditions, where fog would typically result in cooler ambient temperatures. Therefore, this may have resulted from other factors such as heating from the fog machine or a latent heat flux from condensation. Mean VPD in the Fog Chamber ( $0.15\text{ kPa}$ ) was 53% lower than in the Control Chamber ( $0.26\text{ kPa}$ ), indicating that the air was drier in the Control Chamber (Table 6) and this difference was significant ( $P = 0.004$ ).

Leaf wetness in the Fog Chamber ranged from 439 to 467 mV, with a dry baseline of 435 mV, indicating that the simulated fog events successfully wet the leaves of Seaside daisy plants. This information is supplemented by visual observations, where the leaves of plants within the

Fog Chamber appeared wet after fog events. On the contrary, the leaves of plants within the Control Chamber appeared dry.

### **Discussion**

Our results show that simulated fog events increased leaf-level physiological function ( $A$  and  $g_s$ ) of Seaside daisy plants (Fig. 33 & 35). Maximum photosynthesis rates in the fog treatment groups were consistently higher than plants that did not receive fog, regardless of soil water content (Table 6 & Fig. 33). This increase in photosynthesis was greater in non-irrigated plants, which supported our hypothesis that fog would enhance leaf-gas exchange rates, especially when plants did not receive irrigation. It is unlikely that variation in photosynthesis was largely explained by fog drip, due to the negligible increase in shallow soil moisture following simulated fog events. Instead, these results suggest that the primary mechanism to alleviate water stress was likely foliar uptake. These results suggest that fog is a crucial water resource during periods of low soil moisture, such as during the prolonged summertime drought conditions in California. Our interpretation is consistent with other studies that found plant function is strengthened during fog events, despite otherwise dry conditions (Baguskas et al., 2016; Burgess & Dawson, 2004; Eller et al., 2013; Fischer et al., 2009; Vasey et al., 2012). Fischer et al. (2009) conducted a several-year analysis of Bishop pine trees, and found that fog drip and cloud-shading reduced annual drought stress by 56%. Our study strongly suggests that Seaside daisies are efficient at utilizing coastal fog water to support photosynthesis, and this likely translates to the importance of coastal fog on the long-term survival of this species.

We found that plants receiving fog had slightly higher soil moisture than no-fog plants (Table 6 & Fig. 36), which we hypothesize to be fog drip increasing shallow soil moisture. While

there was a significant difference in soil moisture between non-irrigated plants in our study (Fog Only versus Control), there was no significant increase between irrigated plants (Fog and Irrigation versus Irrigation Only), suggesting that fog drip did not matter as much to plant function when soil was already saturated (Table 7 & Fig. 36). Although we did observe slightly higher soil moisture in fog-treated plants, the actual differences in soil moisture were negligible ( $\Delta SM_{(\text{Fog}+\text{Irr})-(\text{Irr})} = 0.0002 \text{ m}^3 \text{ m}^{-3}$ ;  $\Delta SM_{(\text{Fog})-(\text{Ctrl})} = 0.0134 \text{ m}^3 \text{ m}^{-3}$ ), within the instrument's accuracy limits ( $\pm 0.03 \text{ m}^3 \text{ m}^{-3}$ ), and likely did not contribute largely to variation in photosynthesis. Nonetheless, we cannot rule out augmented soil moisture through fog drip entirely, as it may have still contributed to an increase in photosynthesis, particularly in non-irrigated plants (Table 6 & Fig. 33). It is important to note that our study exposed plants to simulated fog for brief 2-hour events; however, in their natural environment plants would be exposed to much longer and more frequent fog events. While fog drip does not appear to be a strong driver of photosynthesis in our study, it is likely still an important water resource for naturally occurring Seaside daisy plants.

We were surprised to find that Fog Only plants had higher photosynthesis rates than Irrigation Only plants (Table 6 & Fig. 33), despite low soil moisture in the Fog Only group (Table 6 & Fig. 36). We hypothesize that the mechanism underlying this pattern is foliar uptake of fog water, which improves the water status of leaves and photosynthesis rates. While there is no evidence from our study which directly tracked foliar uptake, our hypothesis is supplemented by other studies on foliar uptake that shared similar results. Gotsch et al. (2014) found that foliar wetting occurred 34% of the time in a tropical montane cloud forest, and led to a 9% recovery of water transpired during the dry-season. Simonin et al. (2009) found that leaf-wetting supported

photosynthesis of California coast redwood trees, which significantly decoupled the soil-plant continuum. Similarly, Baguskas et al. (2016) found that although plants which received both fog drip and fog immersion had the highest photosynthesis rates, leaf-wetting alone was sufficient in supporting photosynthesis of Bishop pine saplings.

While, logistically, we could not directly measure leaf function during our simulated fog events in order to measure the effects of microclimate, we could still assess the effects of microclimate conditions by comparing treatment groups. By measuring maximum photosynthesis, we were essentially measuring the plant's readiness to perform photosynthesis after being exposed to different treatments. By controlling light levels, we were able to isolate the effects of other microclimate factors such as VPD and temperature. While our study removed the effect of diffuse light, diffuse light from fog would typically improve light-use efficiency of plants and likely also influenced plant function prior to our plant survey measurements (Baguskas et al., 2021). We found that, aside from increased water availability, the positive effects of fog treatments on plant physiology were also driven by differences in microclimate conditions between the Fog and Control chambers. We found a marginally significant relationship between VPD and stomatal conductance ( $P = 0.07$ ). Plants within the Fog Chamber were exposed to lower VPD and displayed higher stomatal conductance rates, compared to plants in the Control Chamber, which was also correlated with higher photosynthesis rates. These results are consistent with Berry et al. (2016), where VPD explained the majority of variation in daytime plant water use in a tropical montane cloud forest. Under ideal, humid conditions, plants are able to function freely, pulling in moisture from the soil and leaf surfaces to conduct photosynthesis. Thus, we also found a significant relationship between soil moisture and

stomatal conductance ( $P = 0.01$ ). In this regard, we successfully simulated foggy conditions and found meaningful relationships between VPD and plant function. However, fog typically reduces daytime temperatures, yet we observed warmer ambient temperatures in the Fog Chamber than in the Control Chamber. We did not anticipate warmer temperatures within the Fog Chamber, although Baguskas et al. (2016) reported an insulating effect as well. Despite our controls on leaf temperature, we found that ambient temperature was significant in explaining variation in photosynthesis ( $P = 0.00$ ) and stomatal conductance ( $P = 0.01$ ). Even so, the difference in ambient temperature between chambers was small ( $1.2\text{ }^{\circ}\text{C}$ ) and likely did not contribute largely to variation in plant physiology. In summary, lower VPD and direct foliar uptake of fog water are the likely mechanisms explaining the patterns of increased photosynthesis and stomatal conductance during fog events.

The results from this study suggest that the ideal microclimate conditions and increased water availability provided by fog events improve the physiological function of Seaside daisy plants. In their natural environment, Seaside daisies are well-adapted to their coastal environments, and likely benefit from both foliar uptake and fog drip as they are exposed to longer, more frequent fog events. However, the results from this experiment are significant because they highlight the role of leaf-wetting and changes in micrometeorological conditions, namely reduced VPD, in supporting plant function, particularly when soil moisture is limited. To the best of our knowledge, there have been no other studies that have explored leaf-level physiology of Seaside daisy plants. Our findings are noteworthy because they provide a better understanding of the relationships between coastal fog and this important nectar resource, with greater implications for effective habitat restoration. Restored habitats in the Green Hairstreak

Corridor each vary in levels of fog inundation and site stewardship, and most plants do not receive frequent irrigation. Based on the results from our study, maximizing fog exposure is a low-cost, natural solution to improve water availability, plant growth, and overall survival of Seaside daisies. From a management perspective, focusing restoration efforts on western-facing, windward habitats in San Francisco, where fog inundation is greater than inland or leeward sites, will likely improve the probability of Seaside daisy survival. Installing fog collectors at restored sites may also help to alleviate water stress during drought periods and provide shelter for butterflies by reducing wind speed. Fog harvesting for irrigation has been demonstrated to be a successful approach, such as in a reforestation effort where seedling survival was greater with fog water inputs (Estrela et al., 2009). Leveraging local topographic variation to harvest fog could be achieved by placing other efficient fog-harvesting plants, such as Coastal Sagebrush, at the top slopes of restored habitats. This would allow gravity fed-irrigation from fog drip to be directed downslope to other plants to support plant function. Increasing fog drip will likely improve survival of important plants which will, therefore, improve habitat quality and help support Green Hairstreak butterflies as well as other pollinator communities.

### **Conclusion**

We demonstrate that coastal fog can enhance the physiological function of Seaside daisy plants, a crucial nectar resource for the rare and threatened Coastal Green Hairstreak butterfly. The results from our study strongly suggest that coastal fog be included in habitat restoration decisions in the Green Hairstreak Corridor, and in coastal, fog-influenced pollinator habitat more broadly. As the climate changes and we see longer, more frequent drought periods, Seaside daisies will likely rely more heavily on coastal fog to support photosynthesis. However, past

studies have shown a historical decline in coastal fog along the Pacific Coast and this pattern is likely to continue (Torregrosa et al., 2014). Climate change will likely impact naturally-growing Seaside daisies in the future as well. Several other studies have shown that limited water availability results in fewer floral resources available to pollinators (Burkle and Runyon, 2016; Carroll et al., 2001), suggesting that this may also impact the pollinators that rely on the Seaside daisy, such as the already-vulnerable Coastal Green Hairstreak butterfly.

## Chapter 5: Conclusion

This research has contributed to our collective understanding of the relationships between the Coastal Green Hairstreak butterfly and its restored urban environment at different spatial and temporal scales. Through the eyes of a butterfly, we have followed the Green Hairstreak through time, learning what contributed to its decline as well as its recovery. And though humans have continuously modified the landscape for hundreds of years, we have learned that we can rectify the past through restoration projects and detailed investigations such as this. Focusing on the Seaside daisy plant, we explored plant-butterfly interactions within their restored habitats and zoomed in on the fine-scale influence of coastal fog on leaf-level physiology. Leveraging results from this study, we provide recommendations on how to improve habitat quality within the Green Hairstreak Corridor.

Our results strongly suggest that coastal fog has a lasting impact on Green Hairstreak habitat quality. At the plant scale, we found that photosynthesis rates increase during fog events, especially when soil is dry. Extrapolating to the habitat scale, it is reasonable to conclude that coastal fog improves the long-term survival of the nectar plants available to butterflies and other pollinators within this habitat, since plants along the coast are well-adapted to foggy environments and rely on coastal fog to alleviate drought stress during the summertime months. At the butterfly scale we found that their behaviors were connected to both microclimate and plant characteristics. We observed a positive relationship between butterfly visitation and nectar reward, finding that butterflies made considerably more visits to the plant with greatest floral display and largest flowers. We believe visits to other plants were determined by their proximity to the largest plant. Therefore, we recommend clustering nectar plants to limit foraging distance

and encouraging plant growth. One way this can be done is to utilize water harvested from coastal fog events to increase water availability to plants. Our study demonstrated that Seaside daisy function (i.e., photosynthesis and stomatal conductance) increased with exposure to fog. By focusing efforts in western-facing habitats, leveraging topographic variation, and installing fog collectors, stewards can increase the amount of water available to plants, therefore improving the survival of plants and overall habitat quality.

The story of the Green Hairstreak is both devastating and heartening. Humans have made a profound impact on the butterflies of San Francisco. These butterflies have persisted through dramatic changes and the restoration efforts made in the past two decades have greatly improved their survival within the dense urban landscape. Our recommendations aim to improve habitat quality and, therefore, the survival of the Coastal Green Hairstreak butterfly. Additionally, it is my hope that readers will now see the world through a different lens and find inspiration in their resilience – and that others may be compelled to act on their behalf.

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