THESIS

# WHERE YOU LIVE MATTERS: EXTREME WEATHER CONDITIONS AMPLIFY TERRITORY QUALITY EFFECTS ON ISLAND BIRD REPRODUCTION

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ABSTRACT

WHERE YOU LIVE MATTERS: EXTREME WEATHER CONDITIONS AMPLIFY TERRITORY QUALITY EFFECTS ON ISLAND BIRD REPRODUCTION

Aspects of territory quality and environmental variation (e.g. rainfall, temperature) are key predictors of reproductive success in birds. However, the interaction between variation in territory quality and extreme weather events on reproduction has seldom been explored. The Island Scrub-jay (*Aphelocoma insularis*), a species endemic to Santa Cruz Island, California, is a highly territorial species where breeding pairs maintain year-round territories that vary in vegetation composition and structure. Using a 15-year dataset (2008-2023), we examined how physical metrics of territory quality and extreme weather conditions affect reproductive output. We found that high-quality territories are characterized by more chaparral/woodland habitat, while low-quality territories have a higher proportion of scrub habitat. In addition, during drought and abnormally hot years, pairs in lower-quality territories experienced significantly reduced reproductive output, often failing to fledge any young at all. Conversely, years of high rainfall and cooler temperatures had a uniformly positive effect, boosting reproductive output for all breeding individuals regardless of territory quality, likely due to increased resource availability. Our findings highlight the importance of how variance in territory quality interacts with drought and high temperatures to disproportionately reduce reproductive output within poor quality territories, but also how wet, cool years can buffer populations by facilitating reproductive success across all territories. As droughts and extreme heat are projected to become more frequent, severe, and prolonged under future climate change scenarios, the reproductive

variance among breeding pairs risks skewing the effective population size and reducing the genetic diversity of this already vulnerable, range-restricted species. This study emphasizes the importance of quantifying variation in territory quality and protecting structurally diverse, high quality habitat types as they may play an outsized role in long-term persistence of territorial species amidst increasing climatic stress.

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# CHAPTER 1. INTRODUCTION

## 1. Background

Extreme weather events are increasing in frequency, severity, and duration (IPCC 2021), yet research has predominantly focused on the long-term effects of gradual warming rather than short-term climatic extremes. Most commonly, extreme weather events are defined relative to their climatological distribution, such as those falling within the upper 90th percentile or lower 10th percentile of long-term historical observations (Zhu & Toth 2001). In avian populations, extreme weather events—especially droughts and heat waves—have been shown to reduce reproductive output by influencing breeding phenology, parental effort, clutch size, and offspring development and survival (Morrison and Bolger 2002; Bolger et al. 2005; Jiguet et al. 2006; Keynan & Reuven 2010; Reichert et al. 2012; Andreasson et al. 2022). However, these studies tend to focus on broad-scale population patterns, while the fine-scale effects of weather variation on demographic processes at the territory level remain underexplored. Given that territory quality influences reproductive success (Högstedt 1980; Stamps 2006; Breininger et al. 2023) and that extreme weather events have the potential to alter resource availability and habitat suitability, it is critical to examine how breeding pairs occupying different quality territories are impacted by environmental extremes.

Most studies investigating how environmental variation influences avian reproductive success have focused either on large-scale habitat fragmentation (e.g. Cox et al. 2013), climate-driven shifts in phenology (e.g. Nilsson et al. 2019), or the role of microclimates within individual territories (e.g. Sofaer et al. 2012). These studies provide valuable insights into how birds respond to environmental change, yet none explicitly examine how territory quality

interacts with climate extremes to shape reproductive performance. For instance, Cox et al. (2013) demonstrated that temperature effects on songbird productivity vary depending on landscape fragmentation, but their study did not account for within-territory resource availability or site fidelity. Similarly, Nilsson et al. (2019) found that white-throated dippers (*Cinclus cinclus*) breeding in high-quality territories, initiated breeding earlier in warm springs, yet this study did not address how territory quality buffered against reproductive declines in extreme drought or precipitation years. While microhabitat conditions have been shown to influence nest success (Sofaer et al. 2012), and extreme climate events can alter habitat availability (Youngflesh et al. 2025), research linking these factors to territory-level reproductive performance remains limited.

Research on climate-driven reproductive dynamics often highlights two main drivers of variation in reproductive performance: environmental conditions and individual quality (Reichert et al. 2017; Sofaer et al. 2012; Breininger et al. 2023). In territorial species, individuals compete for high-quality breeding sites, which typically provide greater resource availability, better nest protection, and increased fitness benefits (Sofaer et al. 2012; Stamps 2006). High-quality sites often buffer individuals from environmental stressors, whereas lower-quality territories may expose birds to increased predation risk and reduced food availability (Whitham 1980; Nilsson et al. 2019). In the context of climate variability, these differences may be magnified, with individuals in poorer-quality territories suffering greater declines in fitness during extreme weather events. Indeed, research suggests that birds in low-quality habitats may experience elevated physiological stress and oxidative damage due to increased energetic demands and limited access to food (van de Crommenacker et al. 2011)

Home range behavior and site fidelity further complicate predictions of how territorial animals will respond to climatic extremes. In species with fixed territories, home range characteristics—including size, vegetation composition, and resource availability—play a key role in shaping reproductive success (Fuller 2012; Sofaer et al. 2012; Cox et al. 2013; Reichert et al. 2017; Reynolds et al. 2019; Shutt et al. 2022; Breininger et al. 2023; López-Peinado et al. 2024; Woodman et al. 2025). While some species may expand their territories in response to resource scarcity (Smith & Shugart 1987; Morellet et al. 2013), others may abandon breeding altogether during particularly unfavorable years (Bolger et al. 2005). The ability of individuals to persist in suboptimal conditions or relocate to higher-quality territories may determine the extent to which extreme climate events lead to population declines or demographic shifts. For example, in the Lark Bunting (*Calamospiza melanocorys*), reproductive success is strongly tied to precipitation, with drought years leading to reduced clutch sizes and nest survival (Skagen & Yackel 2012). Similarly, in the white-throated dipper (*Cinclus cinclus*), breeding success is influenced by a combination of spring temperature, population density, and territory quality, with early breeders experiencing higher reproductive output (Nilsson et al. 2019). These findings highlight the importance of examining the interaction between climatic variability, territory characteristics, and reproductive performance.

A key challenge in linking extreme weather events to reproductive success is distinguishing between direct effects, such as heat-induced nest failure (Olin et al. 2023), and indirect effects, such as changes in prey availability (Cox et al. 2013, Cruz-McDonnell & Wolf 2016). Insectivorous birds, for example, may experience reproductive failures in drought years not because of temperature stress per se, but because lower rainfall reduces insect abundance, limiting food availability for nestlings (Morrison and Bolger 2002; Bolger et al. 2005; Gullett et

al. 2015). In contrast, species that rely on stable food resources, such as acorns or perennial vegetation, may be more resilient to short-term climatic fluctuations (Youngflesh et al. 2025). These differential responses highlight the need to incorporate ecological context—such as vegetation composition and food availability—when evaluating the effects of weather extremes on reproductive success.

One example of ecological context that is particularly critical for understanding organismal responses to extreme weather is the concept of environmental buffering. Environmental buffering refers to the capacity of specific habitats or ecological conditions to mitigate adverse effects of environmental variability on organism performance and survival (Suggitt et al. 2018). Structurally complex habitats, such as dense forest understories, can create stable microclimates that protect organisms from extreme temperatures and reduce the physiological stress associated with fluctuating environmental conditions (Scheffers et al. 2014). These buffered microhabitats, or microrefugia, are increasingly acknowledged as critical for sustaining population viability and species persistence under heightened climatic variability by decoupling local conditions from regional warming trends (Oliver et al. 2015). The concept of environmental buffering is particularly relevant in the study of island-endemic species, where spatial constraints and limited dispersal opportunities may exacerbate the impacts of extreme weather. Island ecosystems often exhibit high site fidelity among territorial species, with individuals returning to the same breeding territories year after year despite environmental fluctuations (Soldatini et al. 2014). However, these same constraints may prevent individuals from relocating to more favorable areas during droughts, heat waves or severe storms, making them particularly vulnerable to climatic extremes. Research on Darwin's finches has demonstrated how severe droughts can lead to population crashes, with individuals in lower-

quality territories experiencing disproportionately high mortality (Boag & Grant 1984). Understanding how territorial birds on islands respond to climatic variability can therefore provide insights into broader ecological and evolutionary consequences of extreme weather events.

Despite the growing body of research on climate change and avian ecology, few studies have examined how extreme weather events interact with territory quality to shape reproductive success in long-lived species. The lack of long-term datasets tracking individual birds with known territory quality has limited our ability to assess how reproductive performance fluctuates in response to climatic extremes. In my master's thesis, I aim to address this gap by leveraging a long-term dataset on an island-endemic passerine, the Island Scrub-jay (*Aphelocoma insularis*). By examining reproductive responses to extreme heat and drought in addition to abnormally high precipitation and cold years, I assessed how territory quality moderates the effects of climate variability on annual fecundity.

### *1.1. Challenges for Range-Restricted Species*

Territorial species with small geographic ranges, such as island endemics, may be especially vulnerable to the combined effects of climate extremes and habitat limitations. Island ecosystems often exhibit high site fidelity – individuals tend to return to the same territory year after year – and limited dispersal opportunities (Soldatini et al. 2014). Unlike species on the mainland that might shift their range or relocate to track favorable conditions, many island birds, despite the ability to fly, cannot easily escape harsh years by moving elsewhere. During extreme droughts or heat waves, an island bird occupying a poor quality territory cannot simply disperse to a wetter or cooler territory because such sites are likely to already be occupied. Moreover, due

to physiological constraints, when high quality territories are all occupied, migrating to a different island, or mainland region, may be impossible. This constraint was famously illustrated by long-term studies of Darwin's finches on the Galápagos—during the severe 1977 drought on Daphne Major, finches experienced a population crash, and individuals in lower-quality feeding territories or with less advantageous beak morphologies suffered disproportionately high mortality (Boag & Grant 1984). That event demonstrated how intense climate events can cause sudden demographic bottlenecks in isolated populations. More broadly, when an entire species is confined to a small area, any increase in the frequency of extreme years poses a significant risk of synchronized reproductive failure or elevated mortality across the entire population (Jentsch et al. 2007).

Additionally, island species often have evolved in relatively predator-free or stable climates and thus may lack resilience to novel stresses (Maloney and McLean 1995; Blumstein 2006). Their small populations also make them inherently vulnerable to stochastic events. For a long-lived, territorial bird, skipping reproduction in a bad year might be a viable individual strategy, but if nearly all individuals skip breeding in the same year, the cohort gap can have lasting effects on population age structure and growth. If such conditions recur frequently, the species' long-term viability comes into question. Understanding how island birds respond to climatic variability is therefore crucial for forecasting their fate under an increasingly variable world and informing conservation actions. For instance, identifying whether some habitats on the island serve as refugia (areas that buffer the extremes) can help managers prioritize those areas for protection. Conversely, if certain habitats consistently fail to support reproduction during droughts, population models may need to account for effectively smaller breeding populations in

those years. Ultimately, examining climate–habitat interactions in an island endemic can shed light on broader ecological and evolutionary dynamics of persistence under environmental stress.

### *1.2. Study System*

This Island Scrub-jay (*Aphelocoma insularis*) is a medium-sized passerine endemic to Santa Cruz Island, a 249-km² island about 32 km off the coast of southern California (Sillett et al. 2012). Island Scrub Oak (*Quercus pacifica*) makes up most of the island's contemporary woody vegetation (Junak 1995). With the entire global population (~2,000 individuals) confined to this single island (Sillett et al. 2012), the Island Scrub-jay has the smallest range of any bird in the Continental United States (Morrison et al. 2014). In fact, the Island Scrub-jay is the only remaining single-island-endemic bird species in the Continental United States (Morrison et al. 2014) and is classified as "Near Threatened" due to its restricted range and small population size, which make it particularly susceptible to environmental change and catastrophes (IUCN 2012). Santa Cruz Island has a Mediterranean climate characterized by cool, wet winters and hot, dry summers, and over the past two decades it has experienced pronounced climatic variability – including severe droughts in 2014 and 2018, and several unusually wet winters (Cayan et al. 2008; Adkins 2023). Such variation provides a natural experiment to examine how a resident island bird copes with swings from drought to deluge.

Ecologically, Island Scrub-jays are territorial, monogamous, and non-migratory (Collins & Corey 2005; Calwell et al. 2013; Delaney & Cheek 2022). Breeding pairs defend year-round territories in a wide mosaic of habitat types found on the island, ranging from oak woodland and chaparral to lower, shrubbier sage scrub and even bishop pine forest patches (Kelsey 1998; Calwell et al. 2013). Average territory size is about 3.5 ha, though it varies widely (from <1 ha

up to ~9 ha) depending on habitat and topography (Atwood 1980; Kelsey 1998; Caldwell et al. 2013). Importantly, only birds that hold territories breed—floating nonbreeders make up roughly half the adult population, comprising mostly younger birds waiting for territorial vacancies (Kelsey 1998; Collins & Corey 2005; Desrosiers et al. 2021). Because high-quality territories are limited, many juveniles delay breeding for several years until they can acquire a territory (Kelsey 1998; Caldwell et al. 2013). Non-territorial individuals roam in flocks through larger home ranges spanning multiple breeding territories but do not reproduce (Atwood 1980, 1990; Mouton et al. 2025). This social system of territorial saturation means reproductive output for the species each year is largely determined by the subset of individuals with access to the best resources. Territory holders typically remain on the same territory across years, exhibiting strong site fidelity and occupying successful nesting areas despite environmental fluctuations (Collins & Corey 2005; Caldwell et al. 2013). Such fidelity can enhance the benefits of knowing a territory well but also means an individual's fate is tied to the fortunes of that patch of habitat.

Previous research on the Island Scrub-jay's breeding ecology provides useful context for this study. Caldwell et al. (2013) conducted a comprehensive study of jay reproduction and reported that despite relatively low nest survival rates (only about 35% of nests fledged young), the ability to re-nest multiple times allowed pairs to fledge on average $1.1 \pm 0.1$ offspring per year. They found that certain habitat features of territories, such as greater vegetation height and dense cover for nest concealment, were associated with higher nest success (Caldwell et al. 2013). This implies that structurally complex habitats (e.g. oak stands or tall chaparral) can improve nesting outcomes by reducing predation or exposure. Interestingly, Caldwell et al. did not detect a direct correlation between the percent chaparral cover of a territory and metrics like clutch size or feeding rate, suggesting that in the years of their study (2008–2011, largely

"normal" rainfall years) vegetative composition per se was not a strong limitation on breeding. However, no prior study has examined Island Scrub-jay reproduction over a long-term series of highly variable years or tested for interactions between territory vegetation and weather conditions. Thus, it remains unknown whether habitat differences might become more important in extreme years outside the range of conditions observed by Caldwell et al. (2013). For example, the potential for chaparral or oak-dominated territories to buffer jays against drought- and heat-induced food shortages was not evaluated in earlier work. Given that the island's climate variability has only intensified (including record-breaking drought and heat in the mid-2010s), there is a pressing need to understand how these birds have fared under recent extremes.

From a conservation standpoint, the Island Scrub-jay is of high concern not only for its limited distribution but also due to looming threats such as disease and climate change. The potential introduction of West Nile virus (WNV) to Santa Cruz Island is considered an imminent threat that could potentially decimate the naïve jay population, as evidenced by ~85% mortality in experimentally infected California Scrub-jays (a closely related mainland species) (Boyce et al. 2011). Planning is underway to mitigate this risk by possibly establishing a second population on neighboring Santa Rosa Island and by vaccinating birds against WNV (Bakker et al. 2020). Santa Rosa Island historically harbored Island Scrub-jays – a fossil jay bone and 19th-century accounts indicate jays historically occurred there – but the species was extirpated, likely in the late 1800s due to human activity (Morrison et al. 2011, 2014). Reintroducing jays back to Santa Rosa (which has a somewhat cooler, more mesic climate and no current jay population) could create an "insurance" population and reduce overall extinction risk (Bakker et al. 2020). Such proactive strategies highlight how critical it is to identify factors that promote the jay's

resilience. If certain habitat types confer advantages under climate stress, ensuring those habitats are preserved or restored on both islands could be key to the species' long-term persistence.

In summary, the Island Scrub-jay exemplifies a range-restricted, territorial bird facing a future of greater environmental uncertainty. Its single-island status, territorial social structure, and recent exposure to extreme weather make it a valuable case study for understanding the nexus of climate variability, habitat quality, and reproductive success in wildlife conservation. This thesis leverages a 15-year dataset of Island Scrub-jay breeding biology (2008–2023) to address this nexus and fill the knowledge gaps identified above.

## 2. Thesis Objectives

I propose that the Island Scrub-jay provides an ideal model system to investigate these issues of climate-driven variability and habitat quality. By investigating how climate-driven environmental variability and habitat heterogeneity interact to affect the reproduction of the Island Scrub-jay, I was able to better identify key drivers of Island Scrub-jay reproduction. Below, I describe my proposed research chapter and specific aims of my second chapter.

First, I quantified the effects of extreme weather conditions on annual reproductive success of Island Scrub-jays. I examined reproduction across a spectrum of climatic conditions, from severe drought and heat years to abnormally wet and cool years, to determine how breeding output (number of young fledged) fluctuates with weather variables. I found that reproductive output significantly increases during wet, cool conditions, whereas annual fecundity drastically decreases during very hot, dry years. These results provide strong evidence that the Island Scrub-jay's reproduction is highly sensitive to local climatic conditions on Santa Cruz Island.

Second, I identified key habitat features linked to high reproductive success. By pinpointing which territory attributes (e.g. denser chaparral/oak cover, larger territory size) are associated with resilient breeding outcomes, this study aims to inform management strategies, such as habitat protection or restoration, that can enhance the species' capacity to withstand increasing environmental variability. Extending upon the results of the study by Caldwell et al. (2013) on Island Scrub–jay reproductive ecology, I discovered that specific habitat types dictated reproductive success for the Island Scrub-jay. I found that territories with a high proportion of oak woodland and chaparral vegetation fledged significantly more young in a given year. Alternatively, territories with more scrub and open grassland habitat had markedly lower annual fecundity. These differences I observed could be linked to variation in food and nest resource availability, as well as the ability to conceal nests from predators (Siikamäki 1998; Morrison & Bolger 2002; Rolando 2002; Sofaer et al. 2013).

Third, I determined whether variation in territory habitat quality mediates reproductive performance and buffers against weather extremes. Using vegetation metrics and territory characteristics, I found that some territories consistently produced more offspring than others and that weather conditions are a key driver of reproductive success in this species. I then assessed whether those differences widen under harsh climatic conditions (drought/heat) and diminish in favorable conditions. Indeed, I found that those breeding pairs occupying lower quality territories exhibited extremely reduced reproductive output especially in drought and high heat years, many of them unable to produce any young at all in these conditions. On the other hand, pairs in high quality territories, while still suffering decreased annual fecundity, produced at least some offspring. However, in years that were exceptionally cool and wet, territory quality no longer directed variation in number of young fledged, but instead all breeding pairs experienced

heightened reproductive output. These results reflect the idea that habitat heterogeneity on the island creates a spectrum of territory quality, and that this variability interacts with interannual weather variation to shape breeding outcomes.

Discerning the complex interplay between habitat variation and weather conditions is critical in aiding our understanding of the drivers of avian reproduction. These thesis results take advantage of both indirect population modeling and direct field observation methods to provide empirical evidence of the abiotic and biotic mechanisms that regulate Island Scrub-jay reproductive performance. I found that territory quality, coupled with climate, impacts the reproductive ecology of this island endemic bird.

### 3. Conservation Implications

The findings of this study confirm that both territory quality and weather extremes are powerful, interacting forces determining Island Scrub-jay reproductive success. Over the 15-year period, annual fledgling production per pair varied considerably in concert with environmental conditions. As predicted, territory habitat played a pivotal role in mediating these effects. During severe drought and heat years, virtually all successful reproduction came from pairs occupying chaparral/oak woodland rich territories, whereas pairs in territories dominated by open scrub or sparse vegetation overwhelmingly failed to fledge any young. In other words, high-quality territories provided a "refuge of reproductive potential" under extreme stress—only jays in these favorable patches managed to breed successfully in the worst years, essentially buffering those individuals from complete reproductive collapse. By contrast, low-quality territories offered little buffer—breeding in those areas largely collapsed in hot, dry conditions. These results support the hypothesis of a habitat-mediated buffering effect where the structural and resource advantages of

certain habitats allow for continued reproduction when climate conditions are poor, whereas birds in poorer habitats are pushed below a threshold needed for any reproductive success. Notably, in years with unusually high rainfall and cooler temperatures, we observed increased fledgling output across all territories, including the typically low-quality ones. Wet, mild years appeared to "level the playing field" by boosting resource availability island-wide (e.g. an insect boom and abundant new plant growth), such that even marginal territories produce young. This pattern highlights that territory quality differences are most pronounced under environmental stress (drought/heat) and less consequential in benign conditions – a clear example of context-dependent effects that aligns with ecological theory (Williams et al. 2010; Youngflesh et al. 2025).

By examining reproduction over an unprecedented range of conditions, this study extends previous Island Scrub-jay research and provides new insights. Caldwell et al. (2013) did not find a strong relationship between chaparral cover and jay reproductive metrics during moderate years, but our long-term analysis reveals that when one includes multiple extreme years, a territory's vegetation composition becomes a decisive factor. Our results make clear that habitat quality is not inherently fixed in its effect, but rather its importance emerges most strongly under severe climate stress. This finding has broad implications for understanding wildlife demography in an era of warming. It suggests that management and research should pay special attention to extreme weather events, as they can unmask latent habitat effects and drive long-term population trajectories more than many "average" years combined (Boag and Grant 1984; Jentsch et al. 2007; Cox et al. 2013; Moritz & Agudo 2013; Nilsson et al. 2019; Lauck et al. 2023).

From a conservation perspective, these findings carry several important messages. First, they highlight the critical role of habitat heterogeneity in buffering population-level reproduction

against climatic extremes. In the context of the Island Scrub-jay, not all the island's habitats are equal – chaparral and oak woodland areas are disproportionately valuable for sustaining the species through drought and heat wave cycles. Protecting and managing these high-quality habitat patches is therefore a high priority for preserving this species. Santa Cruz Island has undergone significant habitat recovery since the removal of feral grazers (sheep and pigs) in the 1980s–2000s, leading to expansion of chaparral and oak cover (Sillett et al. 2012; Yelenik 2018). This vegetative recovery may have directly contributed to increases in the scrub-jay population by improving overall territory quality and food availability. Ensuring that these habitats continue to thrive (for instance, by controlling invasive plants or preventing frequent severe fires that could convert woodland to grassland) will help maintain the natural buffering capacity against droughts. Additionally, our results suggest that during prolonged drought and heat waves, the effective breeding population size shrinks to the subset of pairs in good territories. If future climate scenarios bring more frequent back-to-back extreme years, the long-term genetic and demographic stability of the jay could be undermined as fewer breeders contribute offspring (Frankham et al. 2017). Management strategies should thus consider actions to support breeding in poor quality territories during extremes – for example, providing supplemental water or food in severe drought years might alleviate total breeding failure in those areas and spread reproductive output more evenly. Such interventions could bolster the number of young produced in tough years and reduce bottleneck effects.

Second, our study underscores the importance of climate refugia on the landscape. Even on a small island, there are microclimatic refuges (north-facing slopes, canyon bottoms, dense vegetation stands; Sillett et al. 2012) that remain cooler or moister during heat waves and droughts. These places may offer the jays a better chance to breed successfully when the rest of

the island becomes inhospitable. Identifying and conserving these refugia, and perhaps expanding them (e.g. through planting oaks or enhancing shrub cover in strategic locations), could be a key climate adaptation strategy for the species. This approach is applicable to many range-restricted species and land managers should map habitat variability and protect areas that can serve as asylums during extreme weather events.

Finally, our findings, combined with other threats facing the Island Scrub-jay, point to the need for proactive, multi-faceted conservation measures. As noted, the specter of West Nile virus looms over this sensitive island bird. An extreme climate-induced resource crash could coincide with a disease outbreak, compounding their impacts. The translocation and vaccination strategy proposed by Bakker et al. (2020) — establishing a second population on Santa Rosa Island and inoculating birds against WNV — is a forward-looking plan to reduce extinction risk. Our results strengthen the case for such an approach. Moreover, the "accidental gardener" role of jays (long-distance seed disperse of acorns) could help Santa Rosa's ecosystem recovery, creating a positive feedback for habitat quality (Pesendorfer et al. 2017, 2018). In essence, conserving the Island Scrub-jay in the face of shifting climatic norms will require safeguarding the habitat features that allow it to cope with environmental variability, and mitigating new dangers that could overwhelm its small population. Lessons from this system can inform conservation of other island endemics and territorial species worldwide. By recognizing the interplay of climate and habitat, we can better predict which populations are most at risk and devise strategies — from habitat management to assisted migration — to enhance their resilience in an increasingly variable world.

## 4. Conclusion

In conclusion, this thesis illustrates that even within a single island species, the impacts of extreme weather conditions are not uniform—they are filtered by the mosaic of habitat in which individuals live. The Island Scrub-jay's fate in any given year hinges on an interaction between sky and land – the rains that fall (or fail to fall) and the sheltering chaparral or exposed scrub of its territory. As weather extremes become more frequent in California (Cayan et al. 2008) and beyond, understanding and leveraging such interactions will be essential for conserving not only the Island Scrub-jay, but also the myriad other species that call one small place home.

# CHAPTER 2. WHERE YOU LIVE MATTERS: EXTREME WEATHER CONDITIONS AMPLIFY TERRITORY QUALITY EFFECTS ON ISLAND BIRD REPRODUCTION

## 1. Introduction

Extreme weather events, most commonly defined as being based on an event's climatologically expected distribution (e.g. the top 90% and/or bottom 10% of long-term historical observations), are projected to increase in frequency, severity, and duration as warming temperatures accelerate (Zhu & Toth 2001; IPCC 2021). In bird populations, these extremes—such as droughts and heat waves—often reduce reproductive output by disrupting breeding phenology, constraining parental effort, shrinking clutch sizes, and diminishing offspring survival (Morrison & Bolger 2002; Bolger et al. 2005; Jiguet et al. 2006; Keynan & Reuven 2010; Reichert et al. 2012; Andreasson et al. 2022). However, most research to date has examined broad-scale population patterns and long-term climate trends, while the fine-scale effects of short-term climatic extremes on reproduction at the territory level remain underexplored. Given that territory quality is a key determinant of avian breeding success (Högstedt 1980; Stamps 2006) and that extreme weather can rapidly alter local resource availability and habitat conditions, it is critical to assess how breeding pairs in different-quality territories fare under variable environmental conditions.

Environmental variables and intrinsic habitat quality together drive much of the observed variation in avian reproductive performance (Sofaer et al. 2012; Cox et al. 2013; Reichert et al. 2017; Reynolds et al. 2019; Shutt et al. 2022; Breininger et al. 2023; López-Peinado et al. 2024). In territorial birds, high-quality breeding sites—those with abundant food resources and protective cover—consistently yield higher reproductive success (Siikamäki 1998; Stamps 2006;

Sofaer et al. 2012; Breininger et al. 2023). By contrast, low-quality territories with sparse resources or poor cover expose birds to food shortages and greater predation risk, often resulting in reduced breeding output (Whitham 1980; Nilsson et al. 2019). These disparities in territory quality translate into fitness differences that can be magnified under climatic stress where birds in suboptimal habitats typically suffer sharper declines in fecundity during droughts or heat waves, whereas those in superior territories are buffered. Indeed, individuals constrained to poor-quality territories experience heightened physiological stress and oxidative damage under harsh conditions due to increased energetic demands and limited access to food (van de Crommenacker et al. 2011).

Species' home range behavior and site fidelity further mediate their responses to extreme weather. In species holding fixed territories, home-range characteristics—including territory size, vegetation composition, and resource abundance—strongly influence breeding success (Fuller 2012; Sofaer et al. 2012; Caldwell et al. 2013; Cox et al. 2013; Reichert et al. 2017; Reynolds et al. 2019; Shutt et al. 2022; Breininger et al. 2023; López-Peinado et al. 2024; Woodman et al. 2025). When resources become scarce during a harsh year, some birds compensate by expanding their territory to access additional food (Smith & Shugart 1987). In contrast, others may forego breeding entirely in particularly unfavorable conditions (Bolger et al. 2005). The degree to which individuals can adjust their spatial or reproductive strategies in response to environmental stressors often determines the severity of climate impacts on their reproductive output. For example, in North American grasslands, the Lark Bunting (*Calamospiza melanocorys*) experiences markedly lower reproductive success in drought years, with reduced clutch sizes and nest survival under severe water shortages (Skagen & Yackel 2012). Similarly, in mountain stream habitats, the White-throated Dipper (*Cinclus cinclus*) shows that breeding success is

jointly influenced by spring temperature, population density, and territory quality, where birds that initiate breeding earlier in high-quality territories produce more fledglings than those in lower-quality sites or later-breeding pairs (Nilsson et al. 2019). These cases demonstrate that climatic variability can strongly affect avian reproduction, and that its effects can be mediated by habitat quality and the timing of breeding.

A key challenge in understanding climate impacts on reproduction is disentangling direct effects of weather from indirect, resource-mediated effects (Cox et al. 2013; Cruz-McDonnell & Wolf 2016). Heat waves can directly cause nest failure via thermal stress (Olin et al. 2023), but many reproductive failures in drought years arise indirectly from food scarcity. For example, insectivorous birds often fledge few or no young in droughts not due to heat per se but because reduced rainfall diminishes insect prey, leading to nestling starvation (Morrison & Bolger 2002; Bolger et al. 2005; Gullett et al. 2015). In contrast, species able to exploit stable food supplies (e.g., cached seeds or perennial fruits) tend to be more resilient to short-term climatic fluctuations (Youngflesh et al. 2025). These differential responses highlight the importance of considering ecological context—diet, food availability, and vegetation—in evaluating the effects of extreme weather on reproductive success.

Island endemic birds provide a critical context for examining the interplay of climate and habitat quality, as their limited dispersal opportunities and strong site fidelity can intensify vulnerability to extreme weather. Territorial island species often use the same breeding sites each year (Soldatini et al. 2014), meaning that individuals in poor-quality territories cannot readily relocate when conditions deteriorate. As a result, habitat quality becomes a crucial buffer, or conversely, a source of risk, during extreme conditions. Research on Darwin's finches, for

example, showed that a severe drought in the Galápagos caused a population crash, with birds in lower-quality territories suffering disproportionately high mortality (Boag & Grant 1984).

Despite increasing recognition of climate change impacts on birds, few studies have explicitly investigated how extreme weather events interact with territory quality to shape reproductive success in long-lived, range-restricted species, such as those found on islands. This gap largely stems from the scarcity of long-term, individual-based datasets linking territory characteristics with breeding outcomes across a range of climate conditions. As a result, our understanding of how habitat quality can buffer or amplify the effects of weather extremes on reproduction remains limited. Addressing this knowledge gap is vital as climate extremes become more frequent, since it would improve our ability to predict population responses and inform conservation strategies for vulnerable species.

### *1.1. Hypothesis and Predictions*

This study tests the primary hypothesis that variation in vegetation composition across territories reflects differences in habitat quality, which in turn influences reproductive success in extreme weather years. I assume this relationship between vegetation composition and territory quality arises because denser vegetation cover provides more stable food and nesting resources, as well as better conceals nests from predators and buffers young from environmental extremes (Fuller 2012; Sofaer et al. 2012; Caldwell 2013; Scheffers et al. 2014; Reynolds et al. 2019; López-Peinado et al. 2024). If true, this hypothesis makes several predictions: First, it predicts that in drought and abnormally hot years, breeding pairs occupying lower-quality territories will experience reduced annual fecundity, while those in higher-quality territories will be buffered from the negative effects of weather extremes. Second, this hypothesis predicts that these high-

quality territories will (i) be larger to buffer against extreme weather in the form of providing more resources, (ii) contain a greater density of oak woodland (which provides a critical food source during the non-breeding season) and chaparral vegetation, and (iii) support higher reproductive output across all years despite local climatic conditions.

By focusing on a territorial island-endemic species with a well-documented history of reproductive monitoring, this study provides a unique opportunity to assess the long-term ecological consequences of climate-driven habitat variation. Ultimately, these findings may help inform broader conservation efforts by highlighting the importance of habitat quality in mitigating the impacts of increasing levels of environmental variation on avian populations.

## 2. Material and Methods

### *2.1. Study System*

The Island Scrub-jay (*Aphelocoma insularis*) provides an ideal model species to study the effects of extreme weather on breeding performance. The entire species is endemic to Santa Cruz Island, approximately 32 km off the coast of Southern California, and has experienced several extreme weather events, in the form of extreme temperatures, drought and heavy precipitation over the past 20 years (Cayan et al. 2008; Adkins 2023). The Island Scrub-jay breeding system is also well studied; focal study sites were established in 2007, occupied territories have been mapped and monitored, and hundreds of individuals have been uniquely banded, offering a rare opportunity to work with a long-term dataset. Additionally, the Island Scrub-jay is a relatively long-lived species with an average lifespan of approximately 10 years but can live as long as 20 years (Atwood 1990). Finally, the species is classified as "Near Threatened" on the IUCN Red List (IUCN 2012) due to their restricted range and small population size (~2,000 individuals),

and thus, have been identified as being particularly susceptible to population decline due to climate change.

A unique aspect of Island Scrub-jay ecology is that breeding pairs maintain a year-round territory (mean size = 3.5 ± 0.2 ha), where each territory varies in size (range = 0.4–8.9 ha) depending on the vegetation coverage (Atwood 1980; Kelsey 1998; Collins & Corey 2005; Caldwell et al. 2013). Territory and breeding are strongly correlated such that only those birds who hold territories successfully reproduce (Atwood 1980; Kelsey 1998; Caldwell et al. 2013). However, it is estimated that 50% of the total population is made up of one- to four-year-old "non- breeders" that must wait for a territory holder to die in order to get an opportunity to breed (Kelsey 1998; Derosiers et al. 2021). Unlike breeding pairs that are confined to their territories, non-breeders spend most of the year in small flocks which move throughout the island (Atwood 1980, 1990; Kelsey 1998). Additionally, breeding individuals exhibit higher annual survivorship rates (from 91-94%) compared to non-breeding individuals within the population (Atwood 1980), further reinforcing the importance for individuals to acquire a territory. Throughout the 15-year study period, the island experienced some years of extreme levels of drought and heat waves and most jays on the island were observed forgoing breeding or failing to produce fledged young during those hot, dry years. In contrast, the island has experienced record rainfall and cooler temperatures only a handful of times in the last 20 years. These weather extremes provide an opportunity to examine how extreme precipitation, drought, and fluctuating temperature extremes influence reproductive success in the Island Scrub-jay.

### *2.2. Data Collection*

#### *2.2.1. Reproductive and Territory Monitoring*

Reproductive data were collected over a 15-year period (2008–2023) from three established study plots on Santa Cruz Island – Coches Prietos Canyon (CPC; 115 ha; monitored 2008-2016) in the southeast coastal region of the island, Portezuela (PZ; 124 ha; monitored 2008-2023) in the eastern portion of the Central Valley on the island, and Buena Vista (BV; 52 ha; monitored 2017-2023) in the western portion of the Central Valley on the island (Figure 1). Each plot contained approximately 20 actively monitored territories per year. Territory mapping was conducted using weekly GPS point locations from focal breeding pairs during the breeding season (approximately mid-February to mid-June). Each point count session lasted 20 minutes, with points recorded every five minutes. To minimize temporal bias, a maximum of five territories were surveyed per day, with sampling times for each territory rotated between daily visits. Data collection occurred between 06:00 and 15:00.

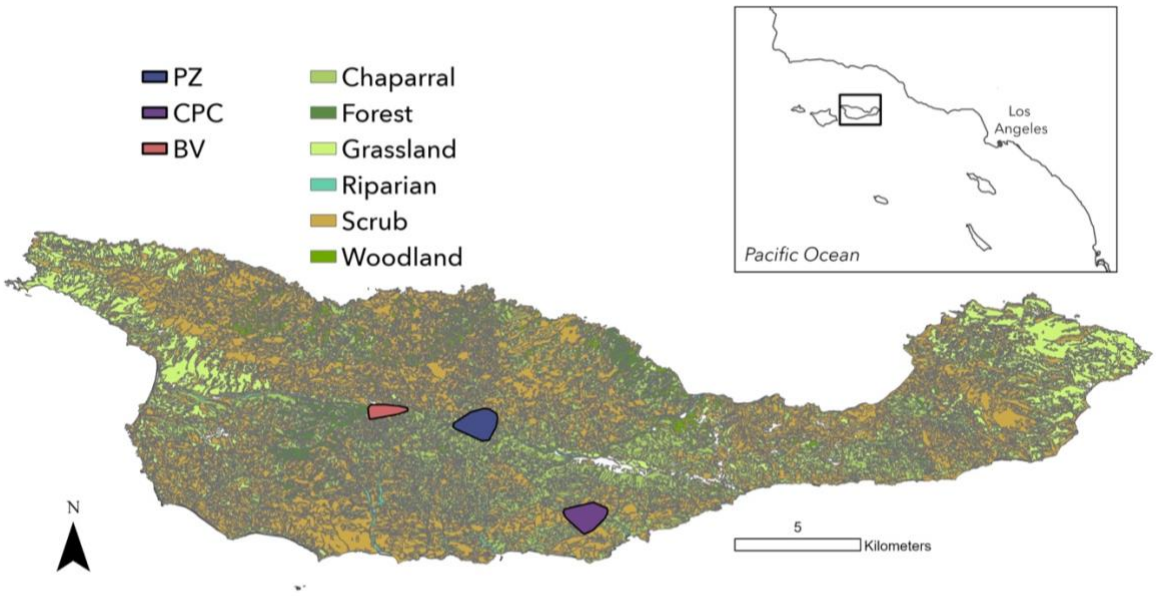


Figure 1. Study area of Santa Cruz Island, California, USA, with sampling plots (colored polygons; *n*= 3) and Island Scrub-jay specific habitat type. Island Scrub-jay breeding activity was observed and recorded at each of the sampling plots from 2008 to 2024. Inset shows the location of Santa Cruz Island (black rectangle) relative to mainland California.

Individuals were captured using box traps baited with peanuts and banded to be easily identifiable via unique combinations of up to six colored plastic leg bands and one aluminum U.S. Geological Survey leg band. Nesting attempts were monitored, and nest fate was determined based on breeding adult behavior and visual confirmation of fledglings. The breeding state of Island Scrub-jays was determined solely through field observations of adult breeder behavior. Individuals that exhibited breeding behaviors each year were unambiguously classified as attempting to breed. Individuals that did not exhibit behaviors indicative of breeding were classified as no attempt at breeding. Additionally, uncertainty of breeding status (in which any attempt was missed by the observer(s)) was scored conservatively as "no attempt". To account for observer bias in our dataset, we filtered the data to only include those breeding pairs in a

given year that we were very certain attempted breeding and either failed or succeeded in producing fledglings (validated through finding the physical nest post-fledge or fail status and getting multiple counts from multiple observers on number of fledglings if the nest fledged). Therefore, our dataset is a conservative representation of the population's annual fecundity, since "no attempt" status datapoints were excluded from the final dataset.

### *2.2.2. Climate Data*

Climate data were obtained from the Western Regional Climate Center, specifically from weather stations located in the Central Valley and Mount Diablo regions of Santa Cruz Island. Monthly total precipitation (in) and mean air temperature (°C) were extracted for the study period. We categorized the climate data into four temporal periods:

- Biological Year (October–April): Represents precipitation and temperature preceding and into the breeding season. This temporal period was also chosen to reflect what we expected to be the most meaningful months of precipitation for Island Scrub-jay reproduction (Moreau 1950; Baxter 1994; Caldwell et al. 2013; Soldatini et al. 2014; Galarza 2020).

- Early (February–March): Captures climatic conditions at the onset of breeding.
- Breeding (February–June): Encompasses climatic conditions during the full breeding season.
- Late (May–June): Examines climatic effects on late-season reproductive success.

Years were classified as drought, normal, or wet based on precipitation thresholds and as hot, normal, or cool based on temperature thresholds. These classifications were determined using

climatological standards and quantile-based thresholds from the literature (Zhu & Toth 2001; NOAA; U.S. Drought Monitor; National Weather Service). Using temperature data extracted from 2007 to 2023, the 20$^{th}$ percentile was designated as the threshold for "Cool" years, while the 80$^{th}$ percentile served as the threshold for "Hot" years. Similarly, the 20$^{th}$ percentile was designated as the threshold for "Drought" years, while the 80$^{th}$ percentile served as the threshold for "Wet" years. The 80$^{th}$ and 20$^{th}$ percentiles capture years of moderate to severe categories of local weather conditions on Santa Cruz Island during the study period, which allowed us to analyze how increasing levels of precipitation and temperature extremes impact Island Scrub-jay reproductive performance.

### *2.3. Territory Mapping and Spatial Analysis*

Territory size, shape, and structure were analyzed using ArcGIS Pro. For all territories with at least five GPS point-count locations recorded over the years they were monitored, we created averaged Minimum Convex Polygons (MCPs) to estimate territory boundaries. To enhance the accuracy of these boundaries, we removed outlier points by applying a 95% MCP method. Although some territories had consistently high numbers of GPS points, others were monitored more sporadically. Despite this resulting in uneven sampling across territories, prior studies indicate that while territory boundaries may fluctuate annually, their centers remain relatively stable (Kelsey 1998; Caldwell et al. 2013). Thus, averaging location data across multiple years allowed us to reliably estimate typical home range sizes and spatial use patterns for each territory. It is worth noting that this method of averaging territory points due to limited data availability may reduce the accuracy of estimating true territory size, particularly by obscuring potential interannual variation in territory shape and size.

Although focal pairs did not consistently occupy the same territories each year due to displacement or mortality, territory boundaries remained stable. Territory size (ha) per MCP was calculated using ArcGIS Pro's Calculate Geometry tool. Territory quality measurements were mapped and modeled using comprehensive vegetation metrics collected on Santa Cruz Island in 2015 in ArcGIS Pro. Vegetation data from 2015 was chosen over the 2005 vegetation data layer for Santa Cruz Island due to its reflection of the most current state of vegetation types and health on Santa Cruz Island following intensive grazing from non-native, introduced ungulates, all of which were removed and eradicated in the 1980s and again in 2006-7 (Sillett et al. 2012; Yelenik 2018). Vegetation data collected in 2015 categorized Santa Cruz Island into 10 habitat types based on the island's main plant communities and identified vegetation guilds at the time of the survey, of which six were relevant to Island Scrub-jay habitat (Caldwell et al. 2013): Chaparral, Woodland, Scrub, Riparian, Pine, and Open Space (Figure 1). Territory quality was assessed by quantifying the proportion of each vegetation category within each MCP. This was done by calculating the total number of individual vegetation polygons within each of the averaged territory MCPs and then converting these into proportions of each vegetation category within each territory using the Python coding interface in ArcGIS Pro.

### *2.4. Statistical Analysis*

Statistical analyses were conducted in the R statistical environment using the R Studio platform (version 4.4.1; R Core Team 2024). The dataset used in our analyses included 732 individual nests monitored over 15 breeding seasons. After removing observations with missing data, we retained 402 nest observations from 178 unique breeding pairs. Each breeding pair could make multiple nesting attempts within a given year (ranging from 0–6 nests per pair annually), resulting in the dataset containing a higher number of nest observations relative to the

number of pairs. For our analyses, an observation was defined as a single nesting attempt by a breeding pair in a given year, with the number of young fledged from each nest as our primary measure of reproductive output. We calculated average reproductive effort and output both overall (across the entire 15-year study period) and comparatively between opposing climatic conditions (hot versus cool, dry versus wet) as well as between territories categorized as either low or high quality. To determine appropriate statistical approaches for analyzing reproductive output, we first assessed the distribution of the number of young fledged per nesting attempt. Using a Shapiro-Wilk normality test, we found that the data significantly deviated from normality ($W = 0.64989$, $p < 0.001$), and further analysis indicated a strong positive skew in this variable (skewness = $1.46 \pm 0.12$). This non-normal distribution justified our decision to use generalized linear mixed models (GLMMs) with a negative binomial distribution, which can appropriately handle overdispersed count data with zero-inflation, as well as non-parametric statistical tests such as the Mann-Whitney U test and Levene's test.

### *2.4.1. Model Selection and Analysis*

To assess the effects of habitat and climate variables on fledging success, generalized linear mixed models (GLMM) were fitted using the 'glmmTMB' package (Brooks et al. 2017). We chose a negative binomial family structure to accommodate the observed overdispersion in our response variable, the total number of young fledged per breeding pair per year (mean = 0.95, variance = 2.46). The number of fledged young served as a proxy for reproductive output since we can definitively know whether a pair fledged offspring as fledglings exhibit distinct juvenile plumage, remain within parental territories for weeks to months post-fledging, and continue receiving parental care (Atwood 1980; Delaney & Cheek 2022). Multicollinearity among vegetation and climate predictor variables was assessed using the Variance Inflation

Factor (VIF) from the ‘car’ package in R (Fox et al. 2019). Due to moderate to high multicollinearity (VIF ≥ 5), Principal Component Analyses (PCA) were utilized to generate component measurements for inclusion in models using the ‘prcomp’ function in base R, with standardization enabled. The GLMMs included territory size, climate variables derived from a PCA (Climate_PC1, Climate_PC2), vegetation variables derived from a PCA (Veg_PC1, Veg_PC2), and interaction terms between primary climate and vegetation PCA components as fixed effects. To ensure consistency in data types, relevant habitat and climate predictor variables were converted to numeric format using the mutate function within the ‘dplyr’ package (Wickham et al. 2023). Random effects included a unique breeding pair ID, created by concatenating aluminum U.S. Geological Survey band codes of paired males and females per year, to control for repeated nesting attempts by the same pairs both within and across breeding seasons, often within the same territories. We followed an information theoretic approach, using Akaike’s Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 1998), to guide model selection and rank competing models. Model fit was assessed through uniformity tests of simulated residuals using the ‘DHARMa’ package in R (Hartig 2024). Predictor variables were standardized (mean = 0, SD = 1) to facilitate direct comparisons of relative importance, and exponentiated coefficients (incidence rate ratios) were calculated for intuitive interpretation of multiplicative effects on the expected reproductive counts. All figures were generated using ggplot2 in R (Wickham 2005).

## 3. Results

### *3.1. Weather Data Classification*

To assess the influence of climatic conditions on reproductive success, years were categorized as "Drought," "Normal," or "Wet" based on biological year precipitation data (Figure

2a). “Drought” years included 2014 and 2018, whereas 2011, 2017, and 2023 were identified as “Wet” years. “Normal” precipitation years included 2008, 2009, 2010, 2012, 2013, 2015, 2016, 2019, 2020, and 2022 respectively. Similarly, years were categorized as "Cool," "Normal," or "Hot" based onbiological year temperature data using percentile thresholds derived from climatological standards (Figure 2b). The classification identified 2010, 2011 and 2023 as “Cool” years, whereas 2013, 2015 and 2016 were classified as “Hot” years. The remaining years, including 2008, 2009, 2012, 2014, 2017, 2018, 2019, 2019, 2020 and 2022, fell within the “Normal” range.

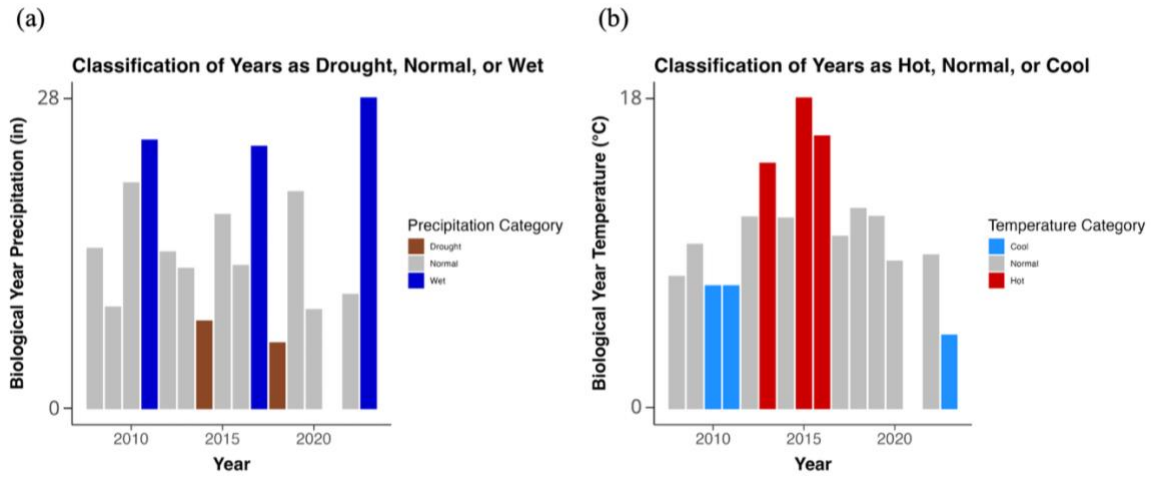


Figure 2. Biological year total precipitation (in; panel a) and average air temperature (°C; panel b) trends across the 15-year study period (omitting 2021 since reproductive data was not sampled that year). Droughts (brown), heat waves (red), abnormally cold temperatures (light blue) and unusually high precipitation events (dark blue) are highlighted in each plot. These classifications were based on an 80th/20th quantile threshold when using long-term precipitation and temperature averages for Santa Cruz Island (1990-2023).

### *3.2. Territory Mapping and Spatial Analysis*

A total of 81 averaged Minimum Convex Polygons (MCPs) were generated in ArcGIS Pro using the Minimum Bounding Geometry tool to estimate territory size and vegetation

composition (34 in PZ, 30 in CPC, and 17 in BV; Figure 3). Territories with fewer than five GPS locations were excluded from the analysis to ensure a more reliable representation of breeding pair movement patterns and territory boundaries.

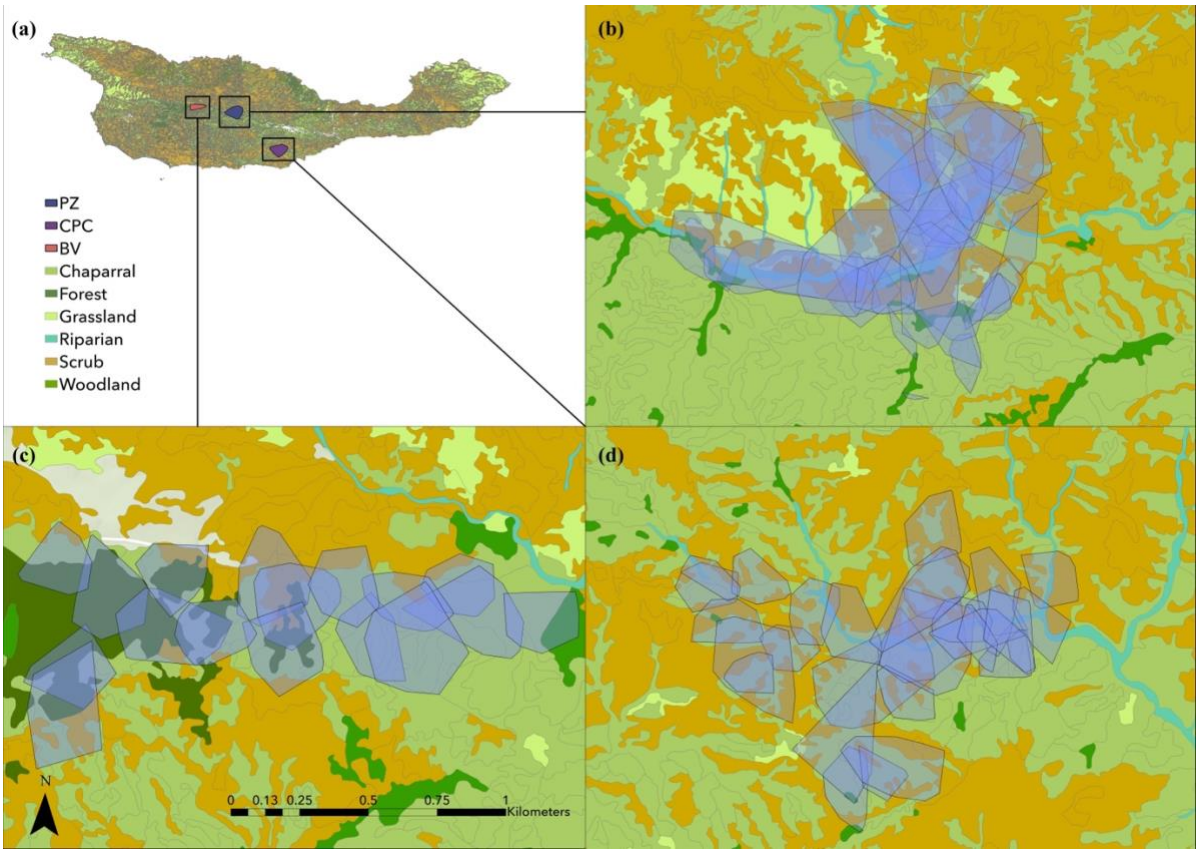


Figure 3. Map of averaged territory Minimum Convex Polygons (MCPs) for each sampling plot. (a) Map of entire Santa Cruz Island with habitat type and sampling plots (black rectangles) shown. (b) Zoomed-in map of Portezuela (PZ) showcasing the averaged territory MCPs (indigo polygons) found within this plot ($n$ = 34). (c) Zoomed-in map of Buena Vista (BV) showcasing the averaged territory MCPs (indigo polygons) found within this plot ($n$ = 17). (d) Zoomed-in map of Coches Prietos Canyon (CPC) showcasing the averaged territory MCPs (indigo polygons) found within this plot ($n$ = 30).

### *3.3. Reproductive Success, Climate, and Habitat Variation*

Among the 402 monitored nests, 192 successfully fledged young, with an overall mean of 1.11 ± 0.87 fledglings per nest across the 15-year dataset. Additionally, 96 breeding pairs out of

the 178 uniquely coded breeding pairs monitored successfully fledged young with a mean of 1.15 ± 1.49 fledglings per pair across the study period. Overall, the average annual nest success rate (those breeding pairs/nests that produced greater than zero fledglings per year) is 37%. To mitigate multicollinearity among climatic and vegetation variables, a Principal Component Analysis (PCA) was conducted separately for each dataset. The climate PCA identified five principal components, with PC1 (Climate_PC1) accounting for 58.27% of the variance and PC2 (Climate_PC2) contributing an additional 17.37%, cumulatively explaining 75.64% of the total variance. The vegetation PCA yielded six principal components, with PC1 (Veg_PC1) accounting for 34.55% of the variance and PC2 (Veg_PC2) explaining 24.43%, together capturing 58.98% of the dataset's variability. Given their substantial explanatory power and based on the loadings, PC1 and PC2 from both datasets were used in subsequent analyses (Table 1). This selection ensures that the most informative aspects of the vegetation and climate data are utilized, enhancing the efficiency and interpretability of our models. The PCA scores were extracted using the 'as.data.frame' function and added to the main dataset using 'bind_cols' from the 'dplyr' package.

Table 1. Principle Component Analyses were conducte for both climate and habitat variables to reduce multicollinearity among the climate and habitat variables used in our models. This table presents the first two principal components derived from separate habitat and climate PCAs (Veg_PC1, Veg_PC2, Climate_PC1, and Climate_PC2) along with their dominant variable loadings, the top three contributing variables by absolute loading, and ecological interpretations. The "Loading (Top Var)" column reports the coefficient of the single variable with the highest absolute loading on each axis, indicating its strength of contribution and correlation to that component. The "Top 3 Contributors" column lists the three original variables whose absolute loadings are greatest, revealing which environmental parameters most strongly define each PC. Absolute loadings near ±1 denote strong positive or negative correlations, while values near zero indicate minimal influence, guiding subsequent interpretation. Veg_PC1 is chiefly driven by Percent.Riparian, Percent.Open.Space, and Percent.Chaparral, representing a gradient from riparian/open habitats to chaparral-dominated sites. Veg_PC2 contrasts woodland and chaparral cover against scrub dominance, with its top contributors being Percent.Scrub, Percent.Chaparral, and Percent.Woodland. Climate_PC1 loads most heavily on Biological.Year.Temp, Breeding.Temp, and Late.Temp, capturing the hot, dry versus cold, wet climatic regime on Santa Cruz Island. Climate_PC2 emphasizes the timing and amount of rainfall versus thermal conditions, with Early.Precip, Late.Temp, and Biological.Year.Precip as principal drivers, signifying inter-annual variability in precipitation timing and seasonal temperature contrasts.

| PC | Loading (Top Var) | Top 3 Contributors | Interpretation |
|---|---|---|---|
| Veg_PC1 | 0.601 | Percent.Riparian<br>Percent.Open.Space<br>Percent.Chaparral | High values indicate riparian and open habitats (e.g. grassland); low values indicate chaparral-dominated sites. |
| Veg_PC2 | -0.776 | Percent.Scrub<br>Percent.Chaparral<br>Percent.Woodland | High values correspond to chaparral and woodland cover; low values represent scrub-dominant areas. |
| Climate_PC1 | 0.462 | Breeding.Temp<br>Biological.Year.Temp<br>Early.Temp | High values reflect warmer, drier years; low scores reflect wetter, cooler years. |
| Climate_PC2 | 0.659 | Early.Precip<br>Late.Temp<br>Breeding.Temp | High values indicate years with strong early-season rainfall versu low late-season temperatures; low values reflect the opposite. |

*3.3.1. Influence of Climate and Territory Habitat Composition on Fledging Success*

Reproductive success varied considerably across climate conditions (Figure 4). "Drought" years exhibited the lowest fledging success, with an average of 0.37 ± 0.91 number of

fledglings per nest, whereas “Wet” years demonstrated the highest reproductive output with an average of 1.66 ± 1.96 fledglings per nest. In “Hot” years, the mean number of fledglings per nest was 0.38 ± 0.99, whereas in “Cool” years, the mean number of young fledged was substantially higher at 1.35 ± 1.83 fledglings per nest. To further evaluate the impact of climatic conditions on the number of fledglings, we utilized both the Mann-Whitney U test and Levene's test, addressing concerns of overdispersion in our observed data. Comparing drought and wet conditions, the Mann-Whitney U test, using the wilcox.test function from base R, revealed a significant difference in the number of fledglings ($W = 1{,}735$, $p < 0.001$), indicating that precipitation levels substantially influence fledgling counts. Using the ‘leveneTest()’ function from the ‘car’ package in R (Fox & Weisberg 2019) further confirmed a significant difference in variance between these groups ($F = 25.37$, $p < 0.001$), suggesting that variability in fledgling numbers differs markedly between drought and wet conditions. Similarly, when assessing hot versus cool temperature conditions, the Mann-Whitney U test indicated a significant difference in fledgling numbers ($W = 4{,}260.5$, $p < 0.001$), highlighting the effect of temperature variations. Levene's test supported this finding, showing significant variance differences between temperature groups ($F = 23.25$, $p < 0.001$).

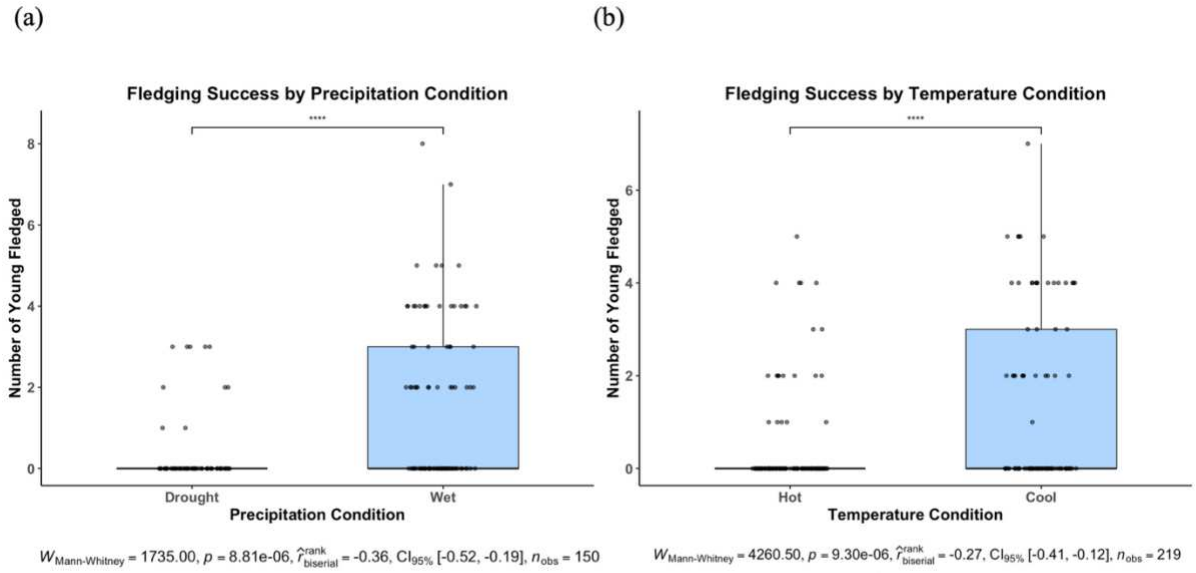


Figure 4. Box plots illustrating differences in reproductive output under contrasting severe climatic conditions, with significance in difference between groups signified by asterisks or n.s. for no significant difference and with Mann-Whitney U test results reported. (a) Reproductive output between breeding pairs during drought years ($n$ = 62) versus abnormally wet years ($n$ = 88). The y-axis shows the number of young fledged, while the x-axis differentiates between precipitation conditions (drought vs. wet). Reproductive success was significantly lower in drought years compared to wet years ($p < 0.001$). (b) Reproductive output between pairs during exceptionally hot years ($n$ = 127) and below-average temperature years ($n$ = 92). The y-axis remains consistent with panel a, while the x-axis represents temperature conditions (hot vs. cool). Although both groups had the same median fledging value (median = 0), reproductive output was significantly reduced in hotter years ($p < 0.001$).

To examine the impact of territory quality on reproductive success, we categorized territories based on their vegetation composition. Specifically, territories with Veg_PC2 scores ranging from 1 to 4 were classified as high-quality, while those with scores between -4 and -1 were deemed as low-quality. This threshold for quantifying territory quality using Veg_PC2 was chosen to better reflect the ecological reality of the Island Scrub-jay, as most territories on the island contain a mix of vegetation types and do not represent the extremes of high or low quality. Analysis revealed that high-quality territories (n = 109) had an average of 0.94 ± 1.73 fledglings

per nest, whereas low-quality territories (n = 105) exhibited a considerably lower average of 0.48 ± 1.18 fledglings per nest (Figure 5). To assess whether fledgling counts differed significantly between high-quality and low-quality territories, we once again utilized the Mann-Whitney U test. The test yielded a W statistic of 6,411.50 and a p-value of 0.04, indicating a statistically significant difference in fledgling counts between the two territory quality groups. Furthermore, to assess the homogeneity of variances in fledgling counts between high-quality and low-quality territories, we conducted Levene's Test. The test produced an F statistic of 5.13 with a p-value of 0.025. This result indicates a statistically significant difference in the variability of fledgling counts between high-quality and low-quality territories. Combined, these results suggest that territory quality has a notable impact on reproductive success in this population.

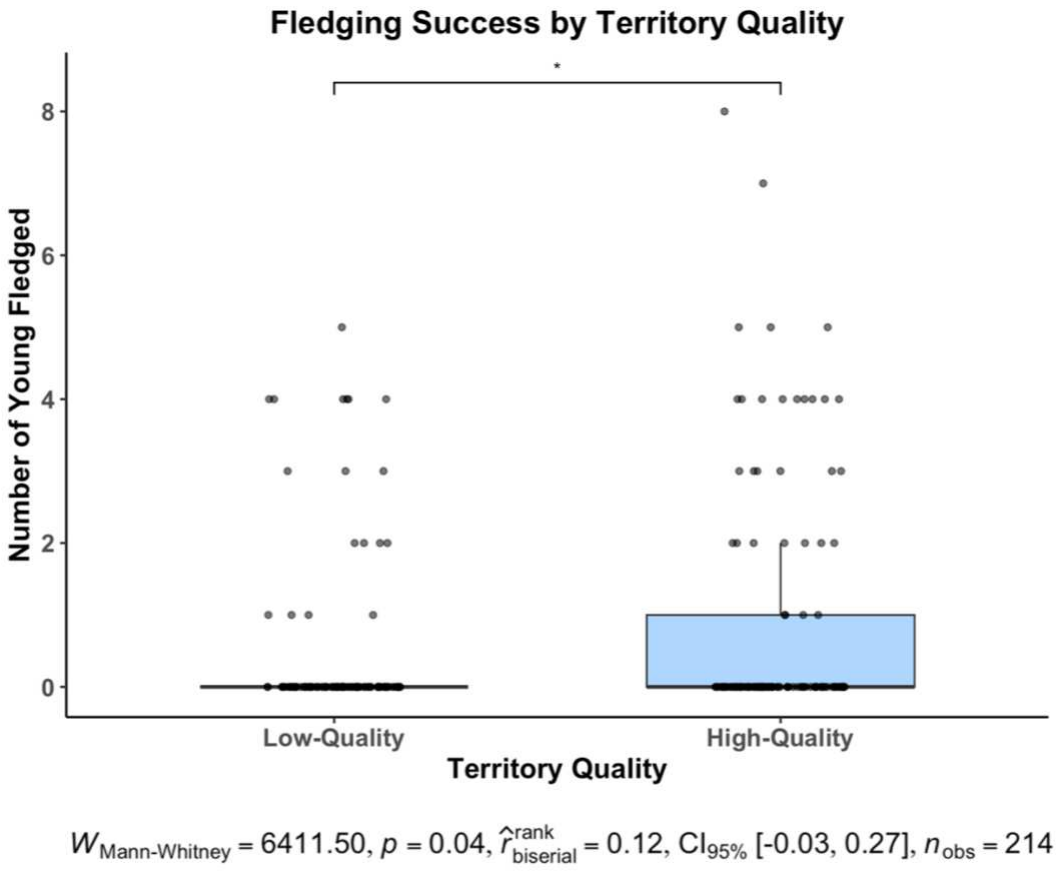


Figure 5. Box plot depicting differences in reproductive output between breeding pairs occupying low- versus high-quality territories, with significance in difference between groups signified by asterisks or n.s. for no significant difference and with Mann-Whitney U test results reported. The y-axis represents the number of young fledged, serving as a proxy for reproductive success, while the x-axis categorizes territory quality (low vs. high). Although both groups share the same median fledging value (median = 0), pairs in high-quality territories ($n$ = 24) exhibited significantly greater reproductive output compared to those in low-quality territories ($n$ = 28; p = 0.04).

### *3.3.2. Model Selection and Analysis*

Negative binomial generalized linear mixed models (GLMMs) were compared across ten candidate fixed-effect structures (Table 2), each retaining a random intercept for Unique.Pair.ID. The top-ranked model included only Veg_PC2, Climate_PC1, and their interaction (6

parameters; QAICc = 1073.09; ΔQAICc = 0.00; weight = 0.232). Adding Veg_PC1 and Climate_PC2 to this interaction yielded a slightly higher QAICc of 1073.75 (8 parameters; Δ = 0.66; weight = 0.167). A purely additive model of Veg_PC2 + Climate_PC1 (no interaction) ranked third (5 parameters; QAICc = 1074.04; Δ = 0.96; weight = 0.144), and inclusion of territory size alongside Veg_PC2 and Climate_PC1 produced QAICc = 1074.32 (7 parameters; Δ = 1.23; weight = 0.125). Models that reintroduced Veg_PC1, Climate_PC2, or additional pairwise interactions fared worse (ΔQAICc ≥ 1.68).

Table 2. Final generalized linear mixed model (GLMM) selection using Akaike's Information Criterion corrected for small sample sizes (AICc), showcasing each model's structure within the "Model" column. Each model is ranked from most parsimonious (top) to least parsimonious (bottom). Number of parameters, adjusted AIC (QAICc), change in QAICc relative to the top model (ΔQAICc), the model's Akaike weight of each model (Wt), and deviance (QDeviance) are also presented. Directly beneath, the cumulative-weight table summarizes the relative support for individual predictors across the entire model set. Cumulative QAICc weights (Σwi) were calculated by summing each model's weight whenever that model includes the focal term.

| Model | Number of Parameters | QAICc | ΔQAICc | Weight | Deviance |
|---|---|---|---|---|---|
| Number.Fledged ~ Veg_PC2 * Climate_PC1 + (1 \| Unique.Pair.ID) | 6 | 1,073.09 | 0.00 | 0.235 | 317.11 |
| Number.Fledged ~ Veg_PC1 + Veg_PC2 * Climate_PC1 + Climate_PC2 + (1 \| Unique.Pair.ID) | 8 | 1,073.75 | 0.66 | 0.169 | 316.06 |
| Number.Fledged ~ Veg_PC2 + Climate_PC1 + (1 \| Unique.Pair.ID) | 5 | 1,074.04 | 0.96 | 0.145 | 317.00 |
| Number.Fledged ~ Territory.Size + Veg_PC2 * Climate_PC1 + (1 \| Unique.Pair.ID) | 7 | 1,074.32 | 1.23 | 0.127 | 316.28 |
| Number.Fledged ~ Veg_PC1 + Veg_PC2 + Climate_PC1 + Climate_PC2 + (1 \| Unique.Pair.ID) | 7 | 1,074.77 | 1.68 | 0.101 | 314.62 |
| Number.Fledged ~ Territory.Size + Veg_PC1 + Veg_PC2 * Climate_PC1 + Climate_PC2 + (1 \| Unique.Pair.ID) | 9 | 1,075.01 | 1.92 | 0.090 | 315.54 |
| Number.Fledged ~ Territory.Size + Veg_PC2 + Climate_PC1 + (1 \| Unique.Pair.ID) | 6 | 1,075.22 | 2.13 | 0.081 | 315.83 |
| Number.Fledged ~ Territory.Size + Veg_PC1 + Veg_PC2 + Climate_PC1 + Climate_PC2 + (1 \| Unique.Pair.ID) | 8 | 1,076.06 | 2.98 | 0.053 | 314.99 |

| Predictor | Cumulative QAICc Weight |
|---|---|
| Territory.Size | 0.351 |
| Veg_PC1 | 0.413 |
| Veg_PC2 | 1.001 |
| Climate_PC1 | 1.001 |
| Climate_PC2 | 0.413 |
| Veg_PC2 * Climate_PC1 | 0.621 |

Cumulative QAICc weights (Σwi) were calculated to quantify the total support each predictor has across the entire candidate model set. In our analysis, Veg_PC2 and Climate_PC1 both achieved Σwi≈1.00, meaning every model with appreciable weight included these two variables providing strong evidence that vegetation structure (Veg_PC2) and the hot, dry versus cool, wet climate gradient (Climate_PC1) are the primary drivers of fledgling production. The interaction between Veg_PC2 and Climate_PC1 accrued a Σwi of 0.62, indicating that models incorporating a vegetation×climate interaction collectively hold 62 % of the total model weight and so there is substantial support for inclusion of this interaction term in our models. Veg_PC1 and Climate_PC2 each summed to Σwi≈0.41, reflecting only moderate support for their inclusion, and Territory.Size had the lowest cumulative weight (Σwi=0.35), implying limited evidence that territory area per se improves model fit.

On the basis of lowest QAICc, parsimony, and cumulative support weight, we therefore selected the Veg_PC2 × Climate_PC1 interaction model as our final specification, excluding non-significant terms (Veg_PC1, Climate_PC2) and territory size to conserve degrees of freedom and maximize inferential power.

Given that the response variable data is zero-inflated, we determined the necessity of incorporating a zero-inflation component into our final negative binomial GLMM. To do so, we employed the 'check_zeroinflation()' function from the R package 'performance' (Lüdecke et al. 2021). This function assesses whether count models are over- or underfitting zeros in the outcome variable. Applying 'check_zeroinflation()' to our final GLMM yielded the following results: 275 observed zeros and 264 predicted zeros, resulting in a ratio of 0.96 with a p-value of 0.26. A ratio close to 1 indicates that the model's predicted zeros closely align with the observed zeros, suggesting that the model is appropriately accounting for zero counts in the data. The p-

value further supports this conclusion, indicating no significant discrepancy between the observed and predicted zeros. Based on these findings, our current negative binomial GLMM adequately accounted for zero-inflation in the data and incorporating an additional zero-inflation component was deemed unnecessary.

A total of 402 nest observations from 178 breeding pairs were analyzed using the top negative binomial GLMM. The results indicated that Veg_PC2 had a significant positive effect on fledgling numbers, suggesting that territories with greater chaparral and woodland cover exhibited higher reproductive success (Figure 6). Conversely, Climate_PC1 had a strong negative effect, indicating that hot, dry conditions significantly reduced fledgling production (Figure 7). Exponentiated coefficients were utilized to interpret the multiplicative effects of predictor variables on fledging success. Veg_PC2 showed a statistically significant 29.9% increase in fledglings, while Climate_PC1 was associated with a highly significant 22.7% decrease in fledgling success (Table 3).

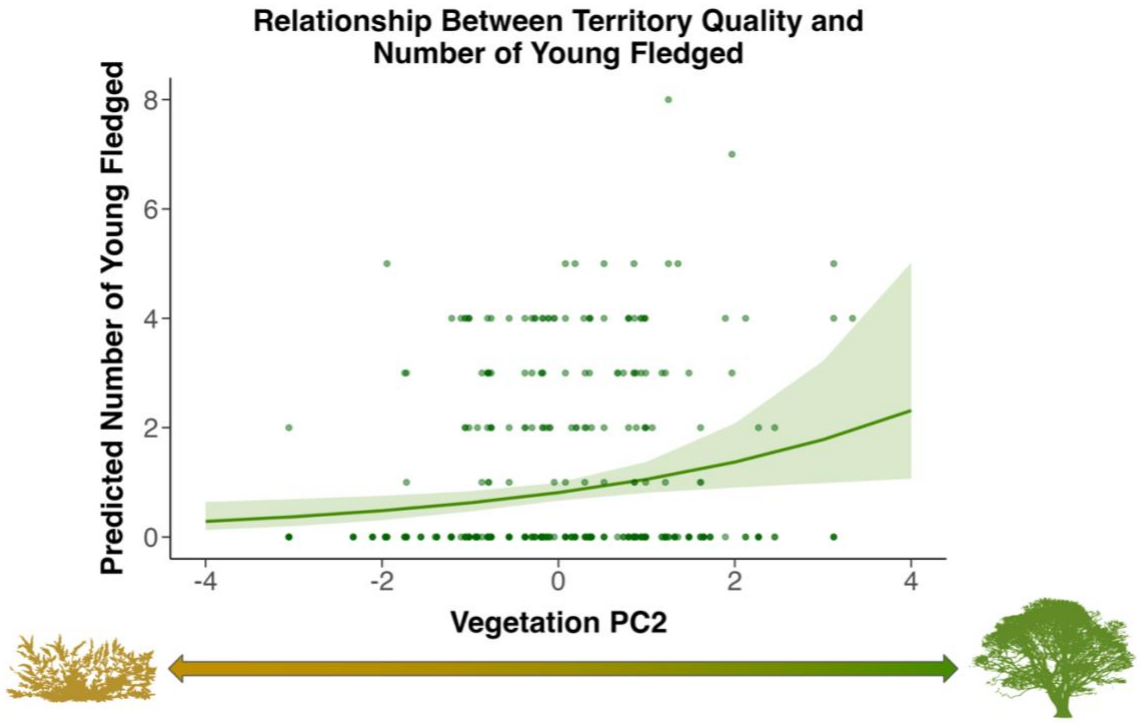


Figure 6. Residual plot showing the relationship between Veg_PC2 and the predicted number of young fledged from the final Generalized Linear Mixed Model. The y-axis displays predicted reproductive output, measured as the number of fledglings per breeding pair per year. The x-axis represents Veg_PC2, a principal component differentiating habitat types, with lower values indicating territories dominated by scrub and higher values reflecting increased cover of chaparral and oak woodland. Breeding pairs occupying higher-quality habitats (chaparral/oak woodland) fledged significantly more young, on average, than those in scrub-dominated territories ($p = 0.008$).

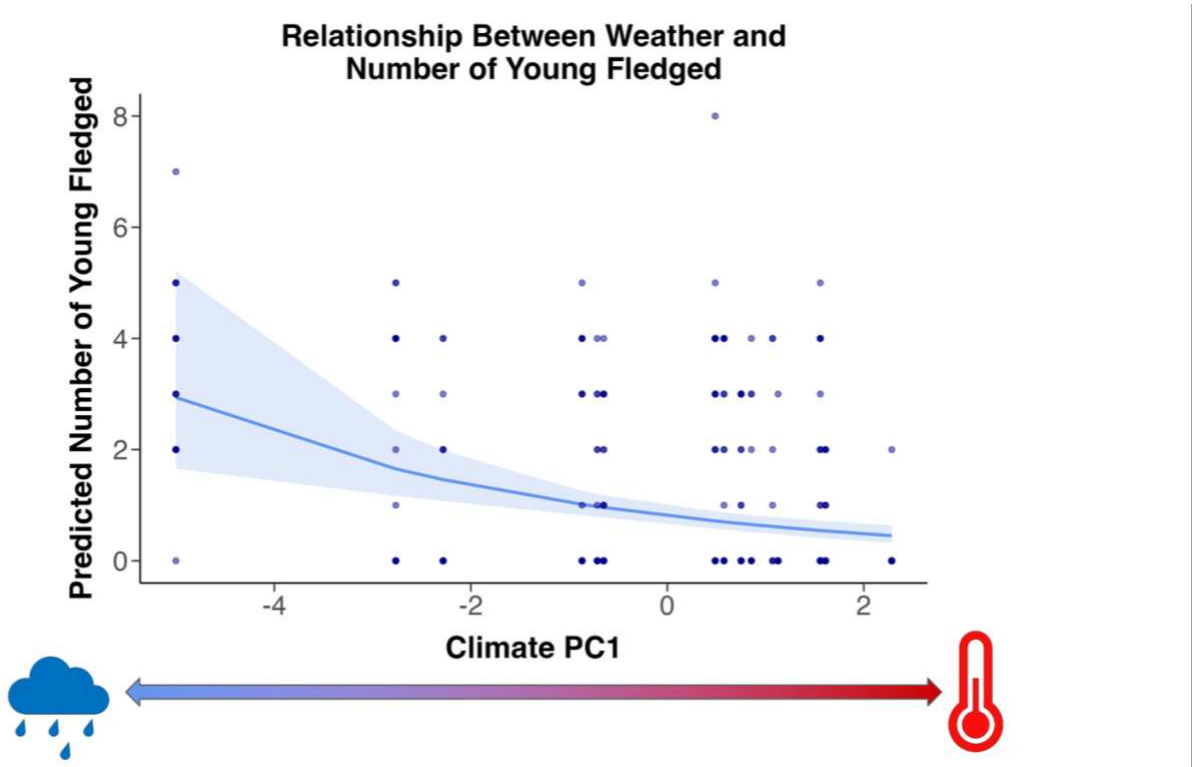


Figure 7. Residual plot showing the relationship between Climate_PC1 and the predicted number of young fledged from the final Generalized Linear Mixed Model. The y-axis displays predicted reproductive output, measured as the number of fledglings per breeding pair per year. The x-axis represents Climate_PC1, a principal component differentiating climatic conditions, with lower values representing cooler, wetter conditions and higher values reflecting hotter, drier weather. Reproductive output is significantly higher during years that are cold and wet, compared to years that are extremely hot and dry ($p < 0.001$).

Table 3. A final Generalized Linear Mixed Model was fitted with a negative binomial family to assess the effects of my focal climate and habitat PCA variables on annual reproductive output (number of young fledged). The Random Effects section reports the estimated variance ($\sigma^2_u$ = $4.61\times10^{-9}$) and standard deviation ($\sigma_u = 6.79\times10^{-5}$) of the random intercept for each unique breeding pair, indicating that after accounting for fixed habitat and climate predictors, there is negligible residual variability among pairs. Because glmmTMB fits Gaussian random effects via a Laplace approximation on the log scale, these small estimates confirm that most variation in fledgling counts occurs within, rather than between, pairs. The model includes 402 observations across 178 levels of Unique.Pair.ID, adesign that supports stable estimation of both fixed and random parameters. Below, the Dispersion Parameter ($\theta = 0.343$) for the negative binomial family (nbinom2) is displayed. In the nbinom2 parameterization, $Var(Y) = \mu + \mu^2/\theta$, so lower $\theta$ values correspond to greater overdispersion relative to Poisson, justifying the choice of a negative binomial model to accommodate extra-Poisson variance. The Fixed Effects section follows, with each coefficient reported on the log scale (link = log), along with its standard error (SE), Wald z-statistic (Estimate/SE), and two-tailed p-value. A Wald z-test is the default method in GLMMs for testing whether each coefficient differs from zero.

| | *Number of Young Fledged* | | |
|---|---|---|---|
| *Predictors* | *Incidence Rate Ratios* | *std. Error* | *Statistic* |
| (Intercept) | 0.83 | 0.09 | -1.82 |
| Veg PC2 | 1.30 | 0.13 | 2.63 |
| Climate PC1 | 0.78 | 0.04 | -4.46 |
| Veg PC2 × Climate PC1 | 1.08 | 0.05 | 1.69 |
| **Random Effects** | | | |
| $\sigma^2$ | | | |
| $\tau_{00\ Unique.Pair.ID}$ | | 0.00 | |
| $N_{\ Unique.Pair.ID}$ | | 178 | |
| Observations | | 402 | |

### *3.3.3. Further Investigation of Local Climate x Territory Quality Interaction*

Additionally, we compared whether the difference in reproductive output was significant across territory quality and climatic conditions using the non-parametric Mann-Whitney U test to account for underdispersion in the residuals from our final GLMM (dispersion = 0.4419, p-value <0.001; applied the 'testDispersion()' function from the 'DHARMa' package in R). Given the small sample sizes after filtering the dataset to only include overlapping poor (–4 to –1) versus high quality (1 to 4) territory PCA values with hot, dry (0 to 2) versus cool, wet (–3 to –5) PCA values, we utilized the exact version of the Mann-Whitney U test to ensure accurate p-value calculations, as recommended for small datasets (Nachar 2008). In poor-quality territories, the analysis yielded a test statistic of W = 193.5 with a p-value of < 0.001 This result indicates a statistically significant difference in the number of fledglings between the two climate conditions, suggesting that climate significantly influences reproductive success in these territories. Conversely, in good-quality territories, the test produced a W value of 223.5and a p-value of 0.98. This implies that, within good-quality territories, climate conditions have a less pronounced effect on reproductive outcomes (Figure 8).

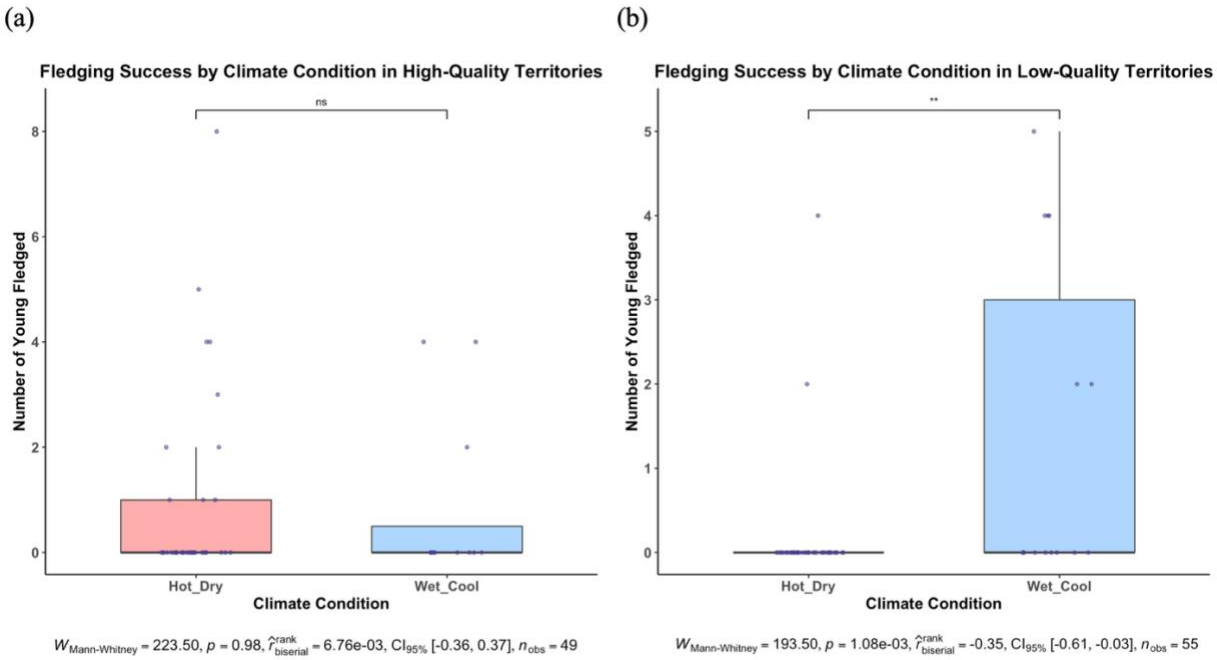


Figure 8. Box plots illustrating differences in reproductive output across contrasting climate conditions and territory qualities, with significance in difference between groups signified by asterisks or n.s. for no significant difference and with Mann-Whitney U test results reported. (a) Comparison of reproductive output for breeding pairs in high-quality territories during extremely hot, dry years ($n$ = 37) versus exceptionally cool, wet years ($n$ = 12). The y-axis shows the number of young fledged, while the x-axis denotes climate conditions. No significant difference in reproductive output was observed between climate conditions for pairs in high-quality territories (p = 0.98). (b) Comparison of reproductive output for pairs in low-quality territories during extremely hot, dry years ($n$ = 40) versus abnormally cool, wet years ($n$ = 15). Axes are consistent with panel (a). Reproductive output was significantly lower in hot, dry years than in cooler, wetter years for pairs in low-quality territories (p < 0.001).

### *3.4. Summary of Results*

To summarize, our final GLMM output, along with our associated post-hoc statistical analyses, showed evidence that pairs occupying high-quality territories, characterized by a higher proportion of chaparral and oak woodland and less scrub habitat, consistently exhibited higher reproductive output compared to those in low-quality territories, regardless of rainfall and temperature variations. However, during drought and high heat conditions, only pairs in high-

quality territories successfully fledged young, while those in low-quality territories consistently failed to produce fledglings (Figure 9).

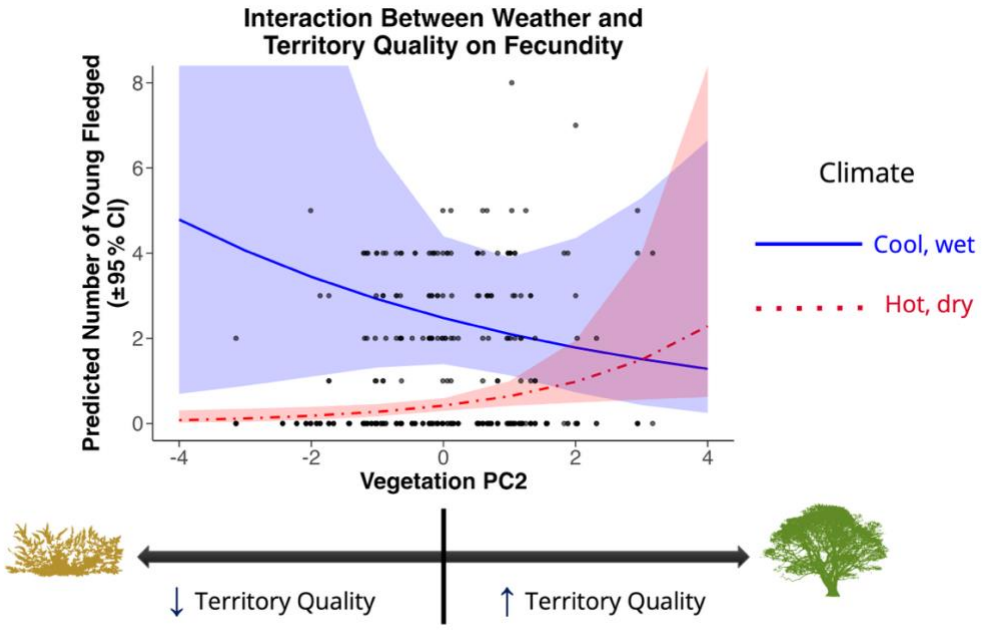


Figure 9. Figure illustrating the interaction between climatic conditions and territory quality on reproductive output, as modeled by a Generalized Linear Mixed Model incorporating an interaction between the primary climate (Climate_PC1) and habitat (Veg_PC2) PCA variables. The y-axis depicts the predicted number of young fledged, used here as a proxy for reproductive success, while the x-axis reflects territory quality, with lower Veg_PC2 values representing low-quality (scrub-dominated) territories and higher values representing high-quality (chaparral and oak woodland) territories. The blue trend line corresponds to cool, wet conditions, whereas the red dotted line represents hot, dry conditions. The high model support for inclusion of the interaction term (Veg_PC2 × Climate_PC1, QAICc = 1073.09; ΔQAICc = 0.00; weight = 0.232; Σwi =0.62) suggests that high-quality territories may partially buffer the negative effects of extreme heat and drought on fledging success.

In addition to using Akaike's Information Criterion for best model fit, we conducted a uniformity test using the 'testUniformity()' function from the 'DHARMa' package in R. This function evaluates whether the residuals from a fitted model follow a uniform distribution, which is an indicator of a well-specified model. The results included a Kolmogorov-Smirnov test that

yielded a test statistic (D) of 0.050186 with a p-value of 0.26 suggesting that there is no significant deviation from uniformity in the residuals. Additionally, the outlier test resulted in a p-value of 0.32 indicating no significant presence of outliers. Overall, these results imply that the model's residuals conform to the expected uniform distribution, supporting the adequacy of the model's fit.

## 4. Discussion

Understanding the factors that shape reproductive success is a fundamental goal of ecological and evolutionary studies because of the implications for population growth, individual fitness, and conservation (Pettifor et al. 2001; Reichert et al. 2012; Mosher et al. 2021; Mouton et al. 2025). However, demonstrating the interactive effects of different environmental factors has proven to be difficult because few datasets allow the resolution to test both the direct and combined effects of local climate and territory quality. The results of this study demonstrate that territory quality and climatic conditions interactively shape the reproductive output of the Island Scrub-jay. High-quality territories—characterized by greater proportion of chaparral and oak woodland habitat—consistently supported higher reproductive success across years, whereas low-quality territories dominated by open scrub habitat suffered markedly lower annual fecundity, especially under extreme drought and heat conditions. Below, we discuss these findings in the context of ecological mechanisms and life-history theory and discuss the non-mutually exclusive impacts of individual versus territory quality on reproduction. We also examine the significance of our findings for the Island Scrub-jay's fitness and conservation amid intensifying environmental variability, and make connections to other vulnerable, territorial species. Finally, we relate our results to relevant studies on habitat quality and weather-driven effects on birds, and propose future research directions.

### *4.1. Territory Quality, Weather Extremes, and Reproductive Performance*

Our data showed a clear habitat-mediated buffering effect; breeding pairs in high-quality territories fledged more young on average and maintained moderate reproductive success even in harsh years, while those occupying mid- to low-quality territories experienced near-total reproductive failure during years of drought and heat waves. In cool, wet years, reproductive success improved across all territories, but even then, pairs in chaparral/oak woodland dominant habitat outperformed those in scrub dominant territories. This interaction between territory quality and annual weather conditions suggests that high-quality territories can ameliorate some negative impacts of environmental extremes on reproduction. Similar patterns of habitat buffering have been observed in other avian populations. For example, forest birds often fare better than those in exposed habitats during heat waves (Kim et al. 2022). A recent analysis of 150,000 nests across the U.S. found that extreme high temperatures halved nesting success in open agricultural lands, whereas forested areas provided a protective canopy that improved nest success under the same conditions (Lauck et al. 2023). In our study, chaparral and woodland vegetation likely provided analogous microclimate refuges—shading nests and retaining moisture—thereby reducing heat stress on incubating adults and nestlings. Dense vegetation may also support more abundant food (invertebrates, acorns) during drought, allowing parents in high-quality territories to continue provisioning their young throughout the breeding season. These findings reinforce the microclimate-buffering hypothesis, which posits that structurally complex, vegetated habitats offer cooler, more stable microclimates that dampen the effects of regional warming on wildlife populations (Kim et al. 2022). Our results thus provide empirical evidence that, for the Island Scrub-jay, territory quality confers substantial resilience to interannual environmental stressors.

Another important mechanism underlying the territory effect is predation and nest concealment. Prior work on Island Scrub-jays found that territories with taller, denser vegetation (e.g., oak chaparral) had lower nest predation rates, contributing to higher overall fledging success (Caldwell et al. 2013). In contrast, open scrub habitats likely leave nests more exposed to predators as well as the elements. During extreme hot and dry conditions, these vulnerabilities are magnified—not only are eggs and nestlings directly susceptible to thermal stress, but parent jays in exposed scrub may face a trade-off between shading the nest versus leaving to forage or thermoregulate themselves, which could result in nest failure.

Indeed, our observations of nearly complete reproductive failure on scrub territories in drought and above average temperature years suggest that many pairs in poor habitat simply did not attempt to breed or, more likely according to our analyses, abandoned efforts—a response consistent with extreme resource limitation. This is in line with life-history theory, such as the fast-slow continuum, for long-lived birds: when conditions for success are bleak, adults may prioritize their own survival over a futile breeding attempt, preserving their energy to try again in a future, hopefully better year (Lack 1968; Hatchwell & Komdeur 2000; Martin & Wiebe 2004; Reichert et al. 2012; Patrick et al. 2022). Such facultative skipping of reproduction in bad years has been documented in other avian systems. Long-term studies in tropical songbirds, for instance, show that long-lived species reduce or forego breeding during severe droughts, a strategy that mitigates adult mortality and buffers the population against environmental stochasticity (Martin & Mouton 2020). The Island Scrub-jay—with a lifespan that can exceed 10 years—fits this pattern of a “slow” life-history strategist (Collins & Corey 1994). Our findings suggest that habitat quality determines how feasible it is for Island Scrub-jays to attempt breeding in a given year. In high-quality territories, resource levels may remain just sufficient,

even in drought and high heat years, for some reproductive output, whereas in marginal scrub territories the threshold for breeding success is not met in extreme years, leading many pairs to forgo breeding entirely.

It is noteworthy that in years with favorable weather (higher rainfall and cooler winter/spring temperatures), reproductive output increased across all territory qualities. This indicates that low-quality territories are not absolute barriers to breeding; rather, they become viable when environmental conditions are benign. In wet, cool years, even scrub-dominated territories produced some fledglings, presumably because water and food were not limiting factors and thermal stress was low. High-quality territories may thus act as "recruitment sources" in a source–sink dynamic, reliably contributing offspring to the population across years, whereas low-quality territories function as sinks that produce young only intermittently (Breininger et al. 2023). Over the 15-year study, we observed that virtually all of the recruitment during the driest, hottest years came from chaparral and oak woodland dominant territories. This disparity underscores how habitat heterogeneity can modulate the impact of increasing environmental variability where extreme conditions amplify the reproductive performance gap between good and poor territories. In practical terms, territory quality provided a form of insurance during stress years—an illustration of the insurance hypothesis whereby habitat diversity and quality stabilize population processes by providing alternative resources or refugia when needed (Kim et al. 2022). Our study extends this concept by demonstrating such insurance effects at the level of reproductive success within a single species and landscape.

It is also worth mentioning that the interaction between territory quality and climatic conditions was not as statistically strong as predicted, which may be attributable to the temporal limitations of the dataset. Although the study spans 15 years, only a limited number of those

years were characterized by severe weather events, such as extreme drought or anomalously high temperatures. As a result, the dataset may lack sufficient variability to detect robust interaction effects, particularly if the buffering role of high-quality habitat only becomes apparent under more frequent or prolonged environmental extremes. Longer-term datasets have been shown to increase statistical power for detecting climate-demography relationships, especially when extreme events are infrequent but ecologically consequential (Williams et al. 2010; Grant & Grant 2011; Youngflesh et al. 2025). Moreover, interactions between habitat and weather conditions may exhibit threshold effects that are not easily captured in shorter time series, where most years fall within relatively moderate environmental ranges (Jentsch et al. 2007). Continued monitoring across a broader spectrum of environmental conditions could possibly improve our ability to detect and interpret the ecological significance of such interactions by increasing our sample size.

### *4.2. Fitness and Population-Level Implications*

The differential breeding success associated with territory quality has important implications for individual fitness and the demographic health of this small island endemic population. High-quality territories not only boost annual reproductive output, but they also buffer lifetime reproductive success for the Island Scrub-jays inhabiting them. A pair consistently occupying a chaparral/oak woodland-rich territory will likely raise many more offspring over their lifespan than a pair consistently stuck in a scrub-dominated territory, especially under increasingly erratic environmental conditions. Although we were unable to look at lifetime reproductive fitness in this study, we can hypothesize that this disparity could lead to strong fitness differences among individuals based on territory tenure. In terms of long-term fitness, individuals that can acquire and hold high-quality territories are at a distinct advantage. It

is conceivable that strong selection pressures may exist for traits that enable winning high-quality territories (whether those traits are aggression, body size, age, gene quality, or earlier arrival to vacancy). Indeed, evidence from this system suggests that older, dominant jays secure the best territories, and younger or subordinate individuals are often left with poorer options or delayed breeding (Kelsey 1998; Caldwell et al. 2013; Desrosiers 2021).

If territory occupancy is semi-permanent (as Island Scrub-jays are territorial year-round and will re-use the same territories until overthrown or dead; Kelsey 1998), then an unlucky subset of the population (pairs occupying mid- to low-quality territories) may chronically contribute few or no descendants to the next generation whenever dry, hot conditions prevail. Meanwhile, a smaller, yet core subset of pairs in high-quality habitat contributes the majority of offspring, particularly in challenging years.

This skew in reproductive contribution can reduce the effective population size (the number of individuals effectively passing on genes) relative to the census population size (the total number of adults in the population). In essence, fewer breeders are responsible for most of the recruitment, which increases variance in reproductive success and can erode genetic diversity over time (Frankham 1995). Repeated frequent drought years could therefore lead to a long-term reduction in genetic diversity and adaptive potential, as the gene pool is repeatedly filtered through the survivors of high-quality territories.

Moreover, prolonged or frequent reproductive failures in a significant fraction of territories may depress the overall population growth rate. The Island Scrub-jay's strategy of forgoing breeding in poor years may be a bet-hedging adaptation for survival, but it comes at the cost of zero recruitment during those periods. If extreme droughts occur in successive years (as

happened during the recent multi-year drought in California; Cayan et al. 2008), the population could experience a dearth of new juvenile hatch years for an extended interval. Our findings during drought years mirror observations by field researchers during the 2012–2015 California drought, when a substantial proportion of Island Scrub-jays did not even attempt to breed for several years (Sillett, pers. comm. 2020; Mouton et al. 2025).

While adult jays can survive and wait out bad years, the temporary halt in reproduction can create an age structure skewed toward older individuals and a potential "gap" in the cohort of young birds. If normal conditions return, those adult birds might still breed again (as we saw reproductive output rebound in the post-drought wet year), but if many older jays die before breeding resumes, the population could decline due to missing younger replacements, especially given the average age of accession to breeding status is 5 years old (Kelsey 1998). In small, closed populations like this island endemic, such temporal clustering of reproductive failure heightens vulnerability to rapid declines. Even if the population size currently appears stable thanks to adult longevity (Mouton et al. 2025), the lack of recruitment reduces the resilience of the population to other threats, since there are fewer young birds maturing to replace natural losses.

Territory quality also interacts with density-dependent processes (Fretwell & Henry 1969). High-quality habitats on the island are limited in area, meaning only a finite number of pairs can occupy chaparral or oak woodland at any given time. Surplus individuals are forced into marginal scrub territories or into non-breeding floater status (Kelsey 1998). In years of favorable weather, those marginal territories at least produce some offspring, but in bad years they add nothing to the population. This dynamic is reminiscent of a buffer effect seen in other

territorial species where lower-quality habitats are occupied when population density is high but contribute proportionally less to reproduction (Osborne & Suárez-Seoane 2007).

Over time, this could lead to an evolutionary premium on competitive ability or on flexibility in breeding decisions. It also raises the question of whether there is any potential for microgeographic adaptation—for instance, are there genetic or behavioral differences in jays that inhabit the pine/oak woodlands versus the open scrub? Recent research has documented habitat-linked genetic and morphological divergence in Island Scrub-jays between different vegetation zones (Langin et al. 2015; Cheek et al. 2022), suggesting that limited dispersal and strong selection in contrasting habitats can drive local adaptation even within this single island. Our findings add a potential fitness consequence to that picture where habitat choice (or availability) has direct impacts on reproductive success, which could reinforce selection for habitat-specific adaptation or preferences.

### *4.3. Reproductive Success Across Landscapes: Linking Individual and Habitat Quality*

One of the initial aims of this study was to determine the extent to which Island Scrub-jay reproductive success under extreme weather conditions was driven by intrinsic individual quality versus extrinsic territory characteristics. In particular, we were interested in whether attributes of the birds themselves (such as age, body size, or body condition) might buffer or amplify the effects of harsh environmental conditions, relative to the influence of the territories they occupied. However, our ability to evaluate individual quality was constrained by the data available. Each bird in our study had only a single set of morphological and condition measurements taken in its lifetime, which provided only a static snapshot of that individual's quality. This limitation prevented us from assessing how an individual's condition might change

over time or in response to varying environmental pressures. As a result, we could not rigorously disentangle the effects of intrinsic traits from extrinsic factors in driving reproductive outcomes.

In avian systems, individual quality is often an important predictor of breeding performance, and failing to account for it can obscure key drivers of reproductive success. For example, it is well documented that reproductive performance improves with parent age and experience in many bird species (Forslund and Pärt 1995). Older or more experienced birds typically fledge more offspring, possibly due to better foraging efficiency, refined parental skills, or occupancy of superior territories gained over time (Margalida et al. 2008). Likewise, birds in superior physiological condition tend to achieve higher reproductive success, as they can allocate more resources to reproduction. Milenkaya et al. (2015), working on a tropical passerine, found that individuals with greater energy reserves (heavier body mass relative to size) produced significantly more fledglings than those in poorer condition. Such findings emphasize that traits like age, body size, and condition—often considered proxies for intrinsic quality—can profoundly influence breeding outcomes.

At the same time, these individual attributes are not independent of the environment. A major challenge in ecological studies is separating the contributions of individual quality from those of territory or habitat quality, because the two are frequently confounded. Individual variation may also arise because of favorable conditions during development, (e.g. the silver spoon effect), which in turn can influence patterns of dispersal and habitat choice (Stamps 2006), mate choice (Candolin 2003), and allocation to parental care and other life history traits (Ratikainen & H. Kokko 2010). Therefore, high-quality individuals may secure high-quality territories, and birds in good condition might better exploit available resources on their territories. Moreover, environmental conditions themselves can directly affect measured

individual quality. Body condition is a dynamic trait that reflects not only an animal's intrinsic state but also recent resource availability and weather conditions (Tonra et al. 2011; Rockwell et al. 2012). For instance, short-term fluctuations in temperature or food supply can cause changes in a bird's mass and fat reserves. A one-time measurement of body condition might therefore capture the transient effects of recent weather or territory resource abundance, rather than an immutable attribute of the individual. In our study, this means that an Island Scrub-jay weighed and measured during a period of food abundance might appear to be a "high-quality" individual, whereas the same bird could exhibit poorer condition measurements if assessed after a prolonged drought. Without repeated measures across different contexts, it is difficult to know whether an individual's breeding success under extreme weather was due to its intrinsic robustness or simply because it was in good condition at the time (which could itself be a result of favorable territory or weather in preceding months).

Our results must be interpreted in light of this limitation. It remains possible that what we attribute to territory effects might, in part, reflect unmeasured differences in the birds occupying those territories. Conversely, any apparent lack of correlation between a bird's one-time measured traits and its reproductive output does not conclusively prove that individual quality was unimportant; it may simply be that our static metrics failed to capture the meaningful variation in quality. Other studies have emphasized the importance of accounting for individual heterogeneity in order to avoid misattributing the causes of reproductive variation. Germain and Arcese (2014), for example, demonstrated the difficulty of distinguishing individual quality from habitat quality in a long-term study of a territorial songbird. They noted that failure to account for persistent individual differences could lead researchers to overestimate the effect of habitat characteristics on breeding success. Similarly, Zabala and Zuberogoitia (2014) argued that in a

long-lived raptor, individual identity explained more variation in fledging success than territory per se, cautioning that territory-based analyses can mask the role of intrinsic differences. In a complementary way, studies that explicitly control for habitat variation provide further evidence of individual effects. Milenkaya et al. (2015) were able to detect a clear relationship between condition and reproductive output in a system where all individuals shared a common foraging habitat (hence minimizing territory-quality differences). Their approach highlights that when habitat differences are held constant, intrinsic quality signals (like body condition) emerge as significant predictors of success. These examples from the literature reinforce the notion that intrinsic and extrinsic factors act in concert, and partitioning their effects requires careful study design.

Given the constraints of our dataset, our study could not fully resolve whether variation in breeding success during extreme weather was predominantly a function of who the breeders were or where they bred. The extreme conditions experienced by the Island Scrub-jays undoubtedly imposed environmental stresses that varied among territories (e.g., differences in food availability, nesting resources, or shelter). Our analysis of territory characteristics (see earlier discussion) captures those spatial differences to some extent. But without a robust measure of each bird's condition upon entering the breeding season—or how it may have deteriorated or improved in response to the weather—means we must be cautious in drawing conclusions about the role of individual quality. It is plausible that high-quality individuals (for example, older jays with prior breeding experience or inherently robust phenotypes due to underlying "high quality" genes) have higher rates of reproductive success during extreme drought than younger or poorer-condition birds. Such patterns have been observed in other systems; older breeders can sometimes buffer reproductive output against environmental

fluctuation due to their experience or physiological resilience (Margalida et al. 2008; Holser et al. 2021). Unfortunately, our study design did not allow us to test these possibilities directly. Any intrinsic advantages among certain jays could not be tracked over time and thus remain obscured within the overall variation we attributed to territory and year effects.

This recognition of our study's limitations has important implications for future research. A key lesson is that long-term data on individual birds would greatly enhance our ability to parse out the drivers of reproductive success. Repeated monitoring of body size metrics (tarsus length, wing chord, tail length, bill length/depth/width), fat stores, or other condition indices for the same individuals across multiple seasons (and before, during, and after extreme weather events) would help distinguish true individual quality from temporal environmental effects. Such a longitudinal approach is widely recommended for studying age-related performance and senescence in wild populations (Nussey et al. 2008), and it would allow us to observe whether, for instance, an experienced jay's breeding output declines less in drought years than a novice's output. Integrating measures of individual health (e.g., hematological indicators, stress hormone levels, or telomere length) could further clarify how intrinsic condition interacts with environmental pressures. Future studies might also consider experimental or quasi-experimental designs, such as translocating individuals between territories of differing quality or supplementing resources in certain territories, to help disentangle these factors. By controlling one factor and observing the outcome, one can begin to see the separate influence of the other; for example, if a bird of known high intrinsic quality still struggles on a poor territory (or vice versa), that would illuminate the relative weight of territory resources.

In summary, while our findings highlight the significant influence of territory quality and extreme weather on Island Scrub-jay reproductive success, we acknowledge that the role of

individual quality remains less clear due to data limitations. The inability to track changes in individual condition over time meant that intrinsic differences could not be fully isolated from extrinsic effects. This constraint likely diluted our power to detect any subtle but real contributions of traits like age or body condition/size to breeding success in extreme years. Nevertheless, the consideration of individual quality is important for a comprehensive understanding of reproductive dynamics. Our results, placed in the context of the broader literature, suggest that future research should explicitly incorporate individual-level monitoring to resolve the interplay between who an organism is and where it lives. Such an approach will be particularly valuable as we anticipate more frequent extreme weather events under changing climatic conditions, where the capacity of individuals to withstand environmental stress may critically mediate population responses. By combining detailed individual data with habitat and climatic variables, researchers can better predict which individuals (or populations) are most vulnerable and which factors most strongly limit reproduction, thereby improving conservation and management strategies for species like the Island Scrub-jay. This study lays the groundwork, and future work building on these insights will help disentangle the intrinsic and extrinsic determinants of reproductive success under increasingly challenging environmental conditions.

### *4.4. Broader Relevance of Territory Quality and Shifting Environmental Pressures on Avian Reproduction*

This research builds upon and extends previous work on Island Scrub-jay ecology and on avian habitat quality more broadly. Caldwell et al. (2013) conducted a foundational study on the breeding biology of this species and found that nest success was influenced by habitat features like vegetation height and concealment, though they did not detect a direct correlation between percent chaparral cover and clutch size or feeding rates. Our results expand on those findings by

demonstrating that, when examined over a gradient of territory types and across variable years, territories with more chaparral/oak woodland do in fact yield higher annual fledgling production. One possible reason for the earlier lack of correlation in Caldwell et al.'s study is that their work focused on immediate nest-level metrics (clutch size, feeding rate) and a period of relatively average environmental conditions. In contrast, our multi-year approach captured dramatic swings in weather conditions, revealing how habitat effects manifest most strongly under environmental stress.

This underscores a key contribution of our study—by examining the interactive effects of habitat and environmental variability, we show that territory quality is not a static determinant of success but one whose importance is context-dependent, emerging most clearly during adverse conditions. This finding aligns with ecological theory suggesting that habitat quality differences often become pronounced when organisms are pushed to the limits of their physiological or resource tolerances (Williams et al. 2010).

Our work also resonates with findings from other territorial bird systems. In the Florida Scrub-jay, a species occupying fire-mediated oak scrub habitat, long-term research has highlighted the role of territory characteristics in reproductive output. Breininger et al. (2023) identified that "strong" (high-quality) territories – typically those in optimal mid-successional scrub with plentiful oak cover – had higher juvenile production, whereas pairs in poorer habitat or at high population densities had lower fecundity. Interestingly, rainfall had only modest influence in that system, while in ours, precipitation was a primary driver of reproductive output. This divergence likely reflects the differing ecological contexts—Florida Scrub-jays breed cooperatively in a relatively stable subtropical climate, whereas Island Scrub-jays breed in isolated pairs within a highly variable Mediterranean climate.

Despite such differences, both systems reinforce the conclusion that safeguarding high-quality habitat is essential to sustaining reproductive output. Our results further suggest that temporal variation shift marginal habitats into effectively non-breeding zones in some years. In this way, our study offers a concrete example of source–sink dynamics modulated not only by habitat but also by the interaction of habitat with short-term environmental extremes.

This demonstrates a critical nuance for conservation planning by which shifting environmental conditions will not affect species homogeneously. Instead, their impacts will be filtered through a landscape mosaic of differing quality, with some areas offering refugia or buffers and others becoming increasingly untenable. Conservation models should therefore integrate habitat heterogeneity and recognize that maintaining microclimatic diversity within landscapes is essential for population persistence under changing environmental regimes (Moritz & Agudo 2013).

### *4.5. Conservation Implications*

From a conservation perspective, these results highlight both a cause for concern and a guide for action. On one hand, climate projections for California indicate an increase in the frequency and severity of extreme weather events, including prolonged droughts and heat waves, which could impose more frequent episodes of reproductive collapse on the Island Scrub-jay population (Cayan et al. 2008; Cal-Adapt). If what we observed in the worst years becomes typical (e.g., multiple heat waves and drought years per decade), the long-term average reproductive rate of the population may decline. A sustained lowering of average reproductive output, combined with possible periodic adult mortality during extreme events (e.g., wildfires, heat stress), could ultimately tip the population into decline. Small island populations have little

room for error; the interactive stressors of limited range and intensifying climatic pressures could synergistically reduce long-term viability.

These findings echo broader patterns in avian conservation research. For example, in the Florida Scrub-jay—a close relative with similarly specialized habitat needs—warmer spring temperatures have extended predator activity periods and reduced annual offspring production by about 25% over the last few decades (Barve et al. 2024). Together, studies like ours and numerous others support the same overarching theme: rapidly shifting environmental conditions are negatively impacting reproduction even in species adapted to environmental variability (Morrison and Bolger 2002; Bolger et al. 2005; Jiguet et al. 2006; Keynan & Reuven 2010; Reichert et al. 2012; Andreasson et al. 2022).

On the other hand, our study points to a potential buffer against these pressures. Maintaining and expanding high-quality habitat could bolster the species' resilience. Habitat management is therefore a key strategy for responding to ongoing environmental shifts. Currently, prime jay habitat on Santa Cruz Island—oak and pine woodlands and chaparral —is recovering following the removal of non-native feral grazers, which has improved breeding conditions for the jays (Sillett et al. 2012; Yelenik 2018). Continuing to protect these areas from degradation (e.g., from invasive species) and facilitating further expansion of these vegetation types could increase the proportion of breeding territories that act as "safe havens" during harsh years.

Beyond the Island Scrub-jay, these insights could hold relevance for other territorial species in similarly fragmented or climatically sensitive systems. Many birds rely on microclimatic refugia during periods of environmental stress, and ensuring access to such

habitats may become increasingly critical. Strategies like habitat enrichment, restoration, and even targeted resource provisioning (with caution) could be explored more broadly as adaptive tools in species conservation.

Additionally, the idea of establishing supplemental populations (e.g., through translocation to nearby islands or protected mainland reserves) could spread risk across a broader spatial area. This is especially relevant in systems where environmental extremes are projected to intensify or where local conditions may vary across relatively small distances. While translocation comes with challenges, it may offer long-term insurance against localized collapse, an approach applicable to many other endemic or range-restricted species under similar pressures. Indeed, plans for translocating a subpopulation of the Island Scrub-jay to establish an assurance population on nearby slightly cooler, wetter Santa Rosa Island are currently being reviewed (Pesendorfer et al. 2018; Bakker et al. 2020; Mosher et al. 2021). Not only would translocating a subset of the Island Scrub-jays to Santa Rosa Island, where the jays historically occurred until the late 1800's (Morrison et al. 2011, 2014), create an assurance population, but the jays themselves could accelerate the restoration of oak woodland on Santa Rosa Island by as much as 200% over the next 100 years through acorn caching behavior (Pesendorfer et al. 2017, 2018). This would act as a positive feedback where the jays would aid in the re-establishment of habitat that helps boost their own reproductive success.

At a minimum, this study highlights the importance of integrating habitat management with real-time monitoring of breeding metrics for the Island Scrub-jay. However, in an era of heightened environmental variability, responsive and informed conservation strategies will be essential—not only for Island Scrub-jays but for other range-restricted, territorial avian populations worldwide facing similar challenges.

### *4.6. Future Research Directions*

While this study has illuminated key factors affecting Island Scrub-jay reproduction, several important questions remain. Given the novel results of this study, future research should aim to deepen our understanding of the mechanisms linking habitat quality, climate, and reproductive outcomes by addressing several specific areas of inquiry.

First, mechanistic studies are needed to investigate the specific resources and microclimatic conditions that distinguish high- from low-quality territories. For example, future work could quantify food availability, such as insect abundance or acorn mast density, and thermal conditions, including nest microclimate temperature and humidity, across habitat types. Such data would clarify how chaparral and oak woodland vegetation buffer jays against drought and heat, whether by providing increased food, cooler nest sites, or both. A detailed understanding of these mechanisms can inform habitat management by identifying which plant species or structural features are most critical to promote in order to support successful breeding.

Second, more research is needed on breeding behavior and physiological responses to extreme conditions. Studies that track behavioral adjustments—such as changes in foraging and nestling provisioning time, time spent finding sources of water, or shade-seeking behavior—in jays occupying different habitat types during heat waves and drought conditions could help elucidate how birds cope with thermal stress and dehydration. At the same time, measuring physiological indicators such as stress hormones (e.g., corticosterone) or body condition in birds occupying high- versus low-quality territories during drought and high heat years would provide insight into the physiological thresholds at which reproduction becomes unsustainable. Bio-loggers or regular health assessments via recapturing known breeders could reveal how resilience

varies between individuals and habitats, offering a clearer picture of the limits of behavioral and physiological plasticity in this species.

Third, continued long-term demographic monitoring of marked individuals will be essential to linking territory occupancy with lifetime reproductive success as well as survival. This research should aim to answer key questions such as whether birds that begin on low-quality territories eventually disperse to better ones and improve their breeding success, or whether they remain in place and simply wait for favorable conditions to return, especially given the high competition for breeding rights. Understanding movement dynamics among territory types would clarify whether low-quality habitats function primarily as spatial sinks or if there is sufficient turnover to allow upward mobility for some individuals. In addition, long-term data would support the development of population viability models that incorporate increasing frequencies of extreme drought and high heat years. Such models could help identify the climatic tipping points at which reproductive rates fall below sustainable levels, thereby informing conservation thresholds and management responses.

Fourth, genetic and evolutionary studies should explore whether habitat-driven differences in reproduction are shaping the population's genetic composition, or whether some individuals have specific genes that are linked to securing higher quality territories (aka higher quality individuals). Prior work has shown habitat-linked genetic divergence in Island Scrub-jays (Langin et al. 2015; Cheek et al. 2022), suggesting the potential for microevolutionary responses to spatial environmental variation. Future studies could test whether alleles associated with successful breeding in hotter, drier scrub environments are increasing in frequency, which would indicate selection for traits conferring resilience under climate extremes. It would also be valuable to assess levels of genetic diversity across birds from different territory types. If birds in

low-quality territories represent a non-random subset of the population, such as younger, smaller, or lower-condition individuals, the consistent lack of reproductive contribution from these birds could eventually erode genetic diversity. Monitoring changes in genetic effective population size over time, especially during repeated drought and above average temperature years, would help determine whether climate-induced reproductive failure is having lasting fitness consequences.

Finally, experimental trials of conservation interventions during extreme weather could test whether active management can increase reproductive success in suboptimal habitats. In particularly dry years, researchers could provide supplemental water or food to a subset of breeding pairs in very low-quality scrub territories and compare their outcomes to those in control territories. Similarly, small-scale habitat enhancements, such as installing artificial shade structures or planting native chaparral or oak woodland vegetation that improve cover, could be piloted to see whether such interventions increase the likelihood of breeding attempts and success. These experiments would help determine whether the reproductive collapse observed in some habitats is reversible through management or whether the birds' decision to forego breeding is a fixed evolutionary strategy. If successful, such interventions could be scaled up as part of a broader climate adaptation strategy for the species if feasible.

Pursuing these research avenues will be critical for developing a comprehensive understanding of how territory quality and climate extremes interact to shape reproductive performance and, ultimately, population persistence in the Island Scrub-jay and possibly for other similar species.

## SUMMARY OF FINDINGS

In conclusion, this study reveals that territory quality and extreme weather act in concert to shape the reproductive performance of the Island Scrub-jay. High-quality territories with abundant chaparral and oak woodland not only promote higher fecundity in average conditions but also offer a critical buffer during drought and heat waves, enabling some breeding success when poor-quality scrub territories fall silent. Conversely, low-quality habitats leave jays acutely vulnerable to climate stress, resulting in breeding stagnation or failure during extreme years. These findings carry significant ecological implications. They illustrate how habitat heterogeneity can mediate climate impacts, with favorable microhabitats serving as refugia that sustain population processes in the face of environmental adversity. For the Island Scrub-jay, the presence of high-quality territories likely cushions the population against complete reproductive collapse during occasional droughts and high heat conditions, but as such events become more frequent under increased warming, the species' long-term viability may hinge increasingly on the availability of these "safe haven" territories and on our efforts to preserve and enhance them.

From a conservation standpoint, our results underscore the importance of protecting and restoring high-quality habitat as a means of climate-proofing the population. Managing Santa Cruz Island's vegetation to favor oak and pine woodland regeneration and dense chaparral stands is not just habitat management, but a direct investment in the species' future reproductive capacity. Additionally, recognizing that a portion of the population (those in marginal habitats) may effectively sit out reproduction, or continue to fail at every nest attempt, in bad years forces us to redefine what a stable population means – it is not enough to count adult breeding jays; we must ensure that sufficient numbers are in environments where they can successfully breed under

both favorable and unfavorable conditions. Proactive measures, potentially including translocations or targeted supplementation during extreme weather, should be evaluated now, so that if climate extremes intensify, we have tools at the ready to prevent consecutive years of zero recruitment from a majority of the breeding population.

In the broader context, this thesis contributes to a growing recognition that wildlife conservation in an era of increasing global environmental pressures must account for the quality of the environment as much as quantity of individuals. The Island Scrub-jay, a flagship endemic of the Channel Islands, has shown us that even a bird adapted to a boom-bust climate regime has its limits, and those limits are largely defined by habitat. By safeguarding the best territories and improving the rest, and by anticipating the challenges that a warming climate will pose, we can improve the odds that this long-lived species continues to thrive on its island home. Ultimately, our study not only advances scientific understanding of how habitat quality and climate extremes interact to affect avian reproduction, but it also provides practical guidance for enhancing the resilience of vulnerable populations in an increasingly extreme world.

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