ABSTRACT

PHARR, LAUREN DANIELLE. Assessment of the Drivers of Partial Brood Loss in the Red-cockaded Woodpecker (*Dryobates borealis*): Density, Weather, and Nestling Condition (Under the direction of Drs. Caren Cooper and Christopher Moorman).

Cooperative breeding offers an exceptional framework for exploring how social and environmental variation interact to shape reproductive outcomes. The federally threatened Red-cockaded Woodpecker (*Dryobates borealis*, hereafter RCW), a long-lived cooperative breeder undergoing active population recovery, provides a rare opportunity to investigate these dynamics through long-term, multi-population datasets. This dissertation examines the ecological and environmental drivers of partial brood loss in RCWs across three well-studied populations in the southeastern United States. In Chapter 1, I tested whether rising partial brood loss was linked to increasing population density. Across all three populations, no evidence supported density-dependent effects on either early or late partial brood loss, suggesting that density increases associated with conservation success are not directly driving reproductive declines. In Chapter 2, I examined whether weather and climate variation influenced early partial brood loss and hatching success. Results revealed limited and site-specific effects of temperature and rainfall, with no broad phenological shifts to buffer against warming, highlighting localized vulnerability to climate change. In Chapter 3, I explored how weather and social factors interact to shape late partial brood loss via effects on brood size hierarchies. Path analysis identified within-brood mass variation as the strongest predictor of partial brood loss, with climate factors acting indirectly to intensify disparities in chick size and survival. Together, these chapters demonstrate that partial brood loss in RCWs is not density-driven but instead emerges through a complex interplay of climate conditions, brood dynamics, and site-specific factors. By integrating long-term monitoring, social structure, and environmental variability, this work advances our

understanding of cooperative breeding systems and provides critical insight into the ecological processes shaping reproductive success in threated species under conservation management.

Assessment of the Drivers of Partial Brood Loss in the Red-cockaded Woodpecker (*Dryobates borealis*): Density, Weather, and Nestling Condition

by
Lauren Danielle Pharr

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APPROVED BY:

Dr. Caren Cooper Committee Chair	Dr. Christopher Moorman Committee Co-Chair
Dr. Nathan Hostetter	Dr. Clyde Sorenson
Dr. Jeffrey Walters External Member	

DEDICATION

This dissertation is dedicated to every individual who has looked at science and not seen a reflection of themselves—see yourself in me, and know that you belong here.

BIOGRAPHY

Lauren D. Pharr is an avian behavioral ecologist and science communicator whose work bridges ecological research and equity in the natural sciences. Growing up in rural North Carolina, she developed an early love for the outdoors, even while rarely seeing people who looked like her represented in science—a perspective that continues to shape both her research and her advocacy. Lauren earned her B.S. in Environmental Biology from Wingate University in 2019 and her M.S. from North Carolina State University in 2021, where she studied the impacts of urban noise and light pollution on birds. In Fall of 2021 she entered NC State's Ph.D. program in Fisheries, Wildlife, and Conservation Biology where she began researching the federally threatened Red-cockaded Woodpecker (*Dryobates borealis*). Her dissertation uses decades of monitoring data to explore how climate and environmental variation influence reproductive success, providing new insights into how cooperative breeders respond to changing conditions and informing conservation strategies. Alongside her research, Lauren is a dedicated science communicator and advocate. She has contributed to *National Geographic* and *WIRED*, appeared on PBS's *Sci NC*, and given more than 60 public and scientific talks. She also co-founded Field Inclusive, a nonprofit working to make fieldwork and outdoor experiences safer and more accessible, particularly for historically excluded communities. Her leadership has been recognized with numerous honors, including the 2023 North Carolina Wildlife Federation Governors Conservation Achievement Award for Young Conservationist of the Year and multiple NC State fellowships. Today, Lauren continues to merge rigorous ecological research with a deep commitment to equity, striving to ensure that future generations of scientists know they belong.

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CHAPTER 1: INTRODUCTION

Linking Social Structure and Environmental Variation to Reproductive Success in a threatened Cooperative Breeder

The Red-cockaded Woodpecker (*Dryobates borealis*, hereafter RCW) is a federally threatened species associated to pine (Pinus spp.) forests of the southern United States. The species' range spans from southeastern Virginia to the Florida peninsula to the south, and west into eastern Texas and Oklahoma. RCWs have a cooperative breeding system consisting of a breeding pair and 0–6 non-breeding adult helpers, which are usually male offspring from a previous year who remain in their natal family group and assist breeders rather than dispersing to a new territory (Walters et al. 1988, Walters and Garcia 2016). In addition to breeders and helpers, adult (≥1 yr old) birds can act as floaters (nonbreeding adults not part of a group). RCWs are habitat specialists, requiring living pines of sufficient age in which to excavate cavities and sparse midstory typically maintain by frequent fire (Conner et al. 2001, Garabedian at al. 2014). RCWs are most common in longleaf pine (Pinus palustris) communities but the species will use other pine types maintained by frequent fire. RCWs lay clutches of 2-5 eggs, and rarely produce a second brood in a year (Jackson 1994, Labranche and Walters 1994a).

The cooperative breeding system has shown to yield greater reproductive success by increasing reproductive productivity of groups (Brown 1987; Emlen 1997; Mumme 1997). For RCWs, increases in group size over time has generally increased reproduction and survival (Walters and Garcia 2016), as is common in cooperative breeding systems (e.g., Lloyd et al. 2009, Preston et al. 2016, Van de Loock 2017). In fact, group size is a strong predictor of cooperative breeder productivity (Lennartz et al. 1987, Walters and Garcia 2016, DeMay et al.

2019). Larger group sizes allow for earlier nesting, which in turn may lead to more successful reproduction in cooperative breeding RCWs (Walters and Garcia 2016). Additionally, larger group sizes lead to more successful RCW fledgling production (Kappes et al. 2020). Helpers can have additive effects on nesting success by increasing the amount of food delivered to nestlings (Komdeur 1994, Doerr and Doerr 2007), especially in species in which nestling starvation and brood reduction is common, and parents do not fully compensate their effort in response to help (Hatchwell 1999, Koenig and Walters 2011).

Despite these social benefits, environmental variability strongly influences reproductive outcomes. Climate change has already altered aspects of RCW reproduction: egg-laying dates have shifted earlier in recent decades, and both clutch size and laying phenology correlate with local annual temperature and rainfall (Schiegg et al. 2002, Garcia et al. 2014). Extreme weather events, such as prolonged cold and heavy rainfall, have acutely reduced nestling survival by limiting adult foraging opportunities and increasing energetic stress (Neal et al. 1993). More subtle variation in temperature and precipitation also shapes within-brood dynamics. Because RCWs incubate asynchronously, chicks often hatch on staggered schedules, producing size hierarchies within broods. Warmer ambient temperatures during laying can accelerate embryonic development in early-laid eggs, further intensifying these hierarchies (Webb 1987, Stoleson & Beissinger 1999, Deeming 2004). During brood-rearing, hot or wet conditions can reduce prey availability, constrain adult foraging efficiency, and alter cavity microclimates, all of which disproportionately affect smaller nestlings, increasing the likelihood of partial brood loss.

Partial brood loss—the death of one or more nestlings before fledging—is a widespread and ecologically important source of reproductive failure in altricial birds (Mock & Parker 1997;

Stoleson & Beissinger 1995). In RCWs, late partial brood loss has risen in recent decades (DeMay et al. 2019). Social structure can mediate these effects: larger groups and more helpers may buffer brood survival by increasing provisioning, shading, and protection. Thus, RCWs represent an ideal system for investigating how environmental and social variation interact to shape within-brood competition and reproductive outcomes.

Intensive management has increased RCW densities across federally protected lands in recent decades, a major conservation success (Walters & Garcia 2016). However, higher densities also alter territorial interactions and group structure (Garabedian et al. 2018, 2019), raising new questions about how population recovery intersects with climate-driven pressures. Understanding how weather, social factors, and chick size variation interact to drive partial brood loss is critical for refining conservation strategies for this threatened cooperative breeder.

To address these challenges, we developed a multi-chapter study at North Carolina State University, supported by the Department of Defense and The Nature Conservancy. Using long-term nest monitoring data, supplemented with additional data collection, our research examines how climate variability, density, and their interaction shape reproductive outcomes in RCWs. This system provides a powerful opportunity to disentangle the interacting effects of density-dependent and density-independent processes on avian population dynamics, with broader implications for the conservation of cooperative breeders under global change.

Introduction to the Dissertation

Avian populations are facing mounting pressures from both environmental change and human-driven habitat alteration. Cooperative breeders, in particular, present unique opportunities to understand how ecological and social factors interact to shape reproduction. The Red-cockaded Woodpecker (*Dryobates borealis*; hereafter RCW) is a federally threatened species and one of the most well-studied cooperative breeders in North America. Despite extensive recovery efforts, RCWs have experienced rising rates of partial brood loss in recent decades, a trend that threatens population productivity and long-term stability. Yet the mechanisms underlying this pattern remain poorly resolved.

Partial brood loss—where one or more chicks in a nest die before fledging—can be shaped by multiple, interacting processes, including group size, population density, environmental variability, and within-brood competition. Identifying the relative contributions of these factors is essential for refining conservation strategies, particularly as RCWs face the dual pressures of population recovery and accelerating climate change.

The focus of this dissertation was to investigate the ecological and social drivers of partial brood loss in RCWs across three long-term study populations in the southeastern United States (Sandhills, NC; Marine Corps Base Camp Lejeune, NC; and Eglin Air Force Base, FL). Using multi-decade nest monitoring datasets, I explored how density, weather, and within-brood dynamics interact to influence reproductive outcomes.

In Chapter 1, I tested whether increasing population density contributed to rising rates of brood loss. Using multiple measures of group size and group density, I assessed whether early or late partial brood loss showed evidence of density dependence.

In Chapter 2, I evaluated how temperature and rainfall shaped reproductive timing and early brood loss. I examined site-specific weather effects on hatching success, brood survival, and the timing of clutch initiation across populations.

In Chapter 3, I investigated within-brood size hierarchies as a mechanism of late brood loss. Using chick mass variation (Coefficient of Variation, CoV), I tested how weather during laying and brood-rearing, together with social factors, influenced brood reduction through effects on chick size inequality.

Together, these chapters provide new insight into the interacting roles of density, weather, and social structure in shaping partial brood loss in RCWs. By integrating long-term demographic monitoring with ecological and social predictors, this work clarifies the mechanisms of reproductive decline in a threatened cooperative breeder and informs conservation strategies under future environmental change.

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CHAPTER 2: INCREASING DENSITY FROM POPULATION RECOVERY DOES NOT EXPLAIN ELEVATED PARTIAL BROOD LOSS IN A THREATENED COOPERATIVE BREEDER

This chapter is in revision in *Ornithological Applications*

Pharr, L.D.; Cooper, C.B.; Moorman, C.E.; Hostetter, N.J.; Sorenson, C.E.; Walters, J.R. (In Revision) Increasing Density from Population Recovery Does Not Explain Elevated Partial Brood Loss in a Threatened Cooperative Breeder. In Revision, *Ornithological Applications.*

Abstract

Partial brood loss in the Red-cockaded Woodpecker (*Dryobates borealis*), a federally threatened cooperative breeder, was not associated with increases in population density. Across three populations — Sandhills, North Carolina; Eglin Air Force Base, Florida; and Marine Corps Base Camp Lejeune, North Carolina — we documented no support for density-dependent effects on either early or late partial brood loss. Using long-term nest monitoring data, we evaluated multiple metrics of group size and group density in relation to early (egg-to-nestling banded at 6-10 days) and late (nestling banding-to-fledgling at age 38-40 days) brood loss. Reproductive outcomes did not vary with density within populations, indicating that the recent rise in partial brood loss, particularly late in the nestling period, is not being driven by increasing density. While both density and partial brood loss have increased over time, these trends appear to be decoupled, highlighting the need to investigate other potential drivers of reproductive decline. Cooperative breeding can buffer reproductive output from density-related pressures through shared parental care, but as densities increase due to conservation-driven population recovery, cooperative breeders may face new or shifting constraints. Variation in reproductive outcomes may be more closely tied to site-specific factors or density-independent pressures such as weather, predation, or habitat quality. As RCW populations continue to grow under ongoing

recovery efforts, understanding the mechanisms behind partial brood loss remains critical for refining conservation strategies. Our results add to growing evidence that density-dependent effects on reproduction are not universal; increasing density, though a conservation success, does not necessarily lead to reduced productivity or increased brood loss.

Introduction

In birds, density-dependent mechanisms play a key role in population regulation, often leading to lower reproductive success and survival at higher densities (Dhondt et al. 1992, Both 1998, Sæther and Bakke 2000, Mallord et al. 2007). Shorter lifespans and faster life histories (e.g., earlier breeding, shorter reproductive windows; Martin 2004) may make temperate terrestrial bird species particularly sensitive to density-dependent constraints. Additionally, temperate regions experience strong seasonality, with resources like food and nesting sites being most abundant during the breeding season (Tökölyi et al. 2012, Watts et al. 2018). As population density increases, competition for these seasonal resources intensifies, potentially exacerbating the negative effects of density dependence on reproduction and survival.

The reproductive strategies of cooperatively breeding species contrast with those of most other temperate bird species. The social behaviors of cooperatively breeding species can help mitigate pressures on survival and reproduction, particularly those related to resource competition, predation, and environmental variability (Emlen 1997). Larger groups often achieve higher reproductive success by sharing parental care and territory defense (Brown 1987; Mumme 1997). More specifically, group members, also called 'helpers', increase overall provisioning at the nest which decreases provisioning efforts of the breeders (Dyer 1983, Emlen & Wrege 1991, Heinsohn 1992, Legge 2000, Brouwer et al. 2006). Cooperative breeding can also confer enhanced predator protection, superior territory defense (Woolfenden & Fitzpatrick 1984), and improved survivorship (Ekman and Griesser 2016, Kerr et al. 2023).

At the same time, cooperative breeding may have costs. Individuals delay dispersal and reproduction to remain as helpers, and reproductive suppression of subordinates and skewed breeder success may occur within cooperative groups. Moreover, group living can result in competition over resources or increased disease and parasite exposure (Cockburn 1998, Koenig & Dickinson 2016). Thus, while cooperative breeding can enhance reproductive success through social support, it also reflects a complex balance of costs and benefits that distinguish it fundamentally from the strategies of most other bird species.

The Red-cockaded Woodpecker (*Dryobates borealis*; hereafter RCW) is a cooperatively breeding species that serves as a case study for understanding how population density affects nestling survival in cooperatively breeding birds over time. Found in the longleaf pine (*Pinus palustris*) ecosystem as well as other southern pine ecosystems around the edges of the range stretching across the southeastern United States, the RCW lives in groups consisting of a breeding pair and 0–6 non-breeding adult helpers. Group size in the RCW is a strong predictor of productivity (Lennartz et al. 1987, Walters and Garcia 2016, DeMay et al. 2019). In recent years, RCW recovery efforts have primarily focused on increasing populations within their existing range, with only limited activities, such as translocations, aimed at expanding the species' range (Walters et al. 2002, U.S. Fish and Wildlife Service 2020). Key conservation strategies, including habitat restoration, artificial cavity creation, and improving habitat quality through frequent prescribed fire, have contributed to higher population densities and larger group sizes (Walters 1991, Walters et al. 2002, Martin et al. 2021). Given that recovery efforts often involve creating cavities near existing groups, these practices have led to RCW densities that are higher than those observed during the mid-20th century (e.g., 1960s–1980s), prior to the implementation of intensive recovery efforts. At elevated densities, individuals may allocate more time and energy to territorial defense due to increased competition for space and resources, potentially reducing foraging efficiency and time allocated to reproduction (Garabedian et al.

2018). Garabedian et al. (2018) documented density-dependent reductions in clutch size and fledging success in RCWs, highlighting how elevated density can negatively impact reproductive output.

RCW populations are experiencing increased rates of partial brood loss, but the causes of this change are unknown. Partial brood loss is greater in RCWs compared to other species of primary cavity nesters in the United States (LaBranche and Walters 1994). Most partial brood loss in RCWs occurs early in the nesting period, with early partial brood loss (EPBL) resulting from a combination of partial hatching and nestling mortality in the first few days after hatching (LaBranche and Walters 1994, DeLotelle et al. 2004). Notably, 90% of nestling loss during the first week occurred within two days of hatching (Sanders 2000). In contrast, late partial brood loss (LPBL) results from nestling mortality alone during the latter half of the nestling period. Although early losses dominate overall patterns related to partial brood loss, findings from this study indicate that LPBL may be increasing — a pattern not previously documented in the published literature. Anecdotal observations and published research have indicated declines in productivity in a portion of the RCW range and that those declines may be driven by increasing density (Garabedian et al. 2014, Garabedian et al. 2018). Understanding at what densities EPBL and LPBL emerge remains an important question for both basic research and conservation efforts.

Here, we analyzed long-term data to examine two measures of density — group density (i.e. number of territories in an area) and group size (i.e. number of adults within a group) — over time in three heavily studied RCW populations to investigate the extent to which these density measures influence EPBL and LPBL in RCWs. Given that higher population densities can increase competition for resources, alter foraging efficiency, and intensify territorial interactions (Walters 1991, Walters et al. 2002, Garabedian et al. 2018, Martin et al. 2021), and populations are experiencing increased rates of partial brood loss, we predicted that 1) increasing group density leads to heightened competition for space and resources and will be associated with higher occurrences of partial brood loss, and 2) greater group sizes (i.e., more individuals to assist with provisioning) and lower group densities will be associated with lower occurrences of partial brood loss. By testing these predictions across multiple populations, we aimed to assess whether density-dependent effects influence reproductive success in recovered RCW populations. Understanding whether current conservation strategies have unintentionally contributed to density-related trade-offs in fitness, and at what densities these effects begin to emerge, will be essential for determining the maximum sustainable densities for RCWs and guiding future management decisions.

Methods

We acquired banding, group composition, and reproduction data from three RCW populations: (1) an inland site in the North Carolina Sandhills (1980–2023; 813 potential breeding groups (PBGs); hereafter Sandhills), (2) a site on the central coast of North Carolina at Marine Corps Base Camp Lejeune (1986–2022; 136 PBGs; hereafter Lejeune), and (3) a Gulf Coast Florida panhandle site at Eglin Air Force Base (2006–2023; 533 PBGs; hereafter Eglin, Figure 1). All three areas were managed under long-term conservation plans designed to create and maintain high-quality habitat for RCWs, with the exception of some privately owned parcels within the Sandhills study area that are not formally managed for RCWs. Briefly, monitoring is facilitated by the resin-coated cavities excavated in living pines characteristic of this species, which are highly conspicuous, and by the long-term stability of territories. All territories in the study areas were visited prior to each breeding season to determine whether it was occupied, indicated by the presence of at least one active cavity tree. Thereafter, cavities were inspected within each active territory every 7-11 days to detect and monitor reproductive attempts. At 5-10 days post hatching, nestlings were banded with a unique combination of color bands. Groups were followed post-fledging to determine the identity and sex (based on sexually dimorphic crown patches) of fledged young. Color-banded adults were identified to obtain group size and composition, and each individual was assigned a status (e.g., breeder, floater, or helper) based on behavioral observations and their age. Unbanded adults immigrating into the study areas were captured from their roost trees and color banded. Refer to Walters et al. (1988) for a more detailed description of data collection. We were only able to include years where complete data were available for all three sites; thus, the site-years included in the analysis were variable based on the year data collection started for each site, with each site being analyzed separately for this analysis.

To assess population density and its effects on EPBL and LPBL, we used two metrics: group density (measured via Thiessen polygon size) and adults per hectare as a measure of group size (Garabedian et al. 2018). We used Thiessen polygon size as a spatial proxy for group density, with smaller polygons interpreted as reflecting higher local density and larger polygons indicating lower density (Garabedian et al. 2018). For each PBG, we used the sf package in R (Pebesma 2018) accessed through R v4.2.2 (R Core Team 2024) to generate Voronoi (Thiessen) polygons based on the UTM coordinates of each active cluster center. We used the same mean cluster center for each PBG for each monitoring year. For all three sites in 2023, we had complete records of the cluster centers for every PBG that was monitored over the extent of the study. Using these 2023 centers, we calculated 800-m (200-ha) buffers around each centroid to approximate Thiessen polygons for each cluster by year, ensuring that each cluster was assigned a unique group ID based on proximity to its respective centroid (Garabedian et al. 2020). The Voronoi tessellation split space equidistantly between neighboring centroids, resulting in smaller polygons when the number of groups in the area increased.

For each year and PBG, we recorded the breeder male and male helpers, breeder female and female helpers, and floaters (i.e., individuals that have dispersed from their natal territories but have yet to find a new territory or group to join). We calculated group size as the sum of male and female breeders and helpers and excluded floaters. We divided the group size by the Thiessen polygon area to get annual adults per hectare.

For each PBG, we included data on first nest attempts, clutch size, number of nestlings, and number of fledglings. We defined EPBL as occurring during the incubation period (ranges from 11-14 days) to when the nestlings hatched and were banded at 6-10 days old. We defined LPBL as occurring from the banding stage of the nestlings until they fledged at 38-40 days old. We counted eggs that did not hatch into nestlings and nestlings that died before banding as EPBL. Nests with a single egg were excluded because it is not possible to distinguish between whole brood loss and partial brood loss for one-egg clutches. Nests with more than five eggs were also excluded, as they are uncommon and typically are produced by co-breeding females and thus likely have different hatching dynamics than regular nests. Additionally, nests in which no eggs hatched were categorized as whole brood loss and hence were not included in the analysis. For EPBL, we set a binary indicator to 0 if all eggs hatched and all nestlings were banded, and 1 if not. Because our monitoring schedule did not allow us to consistently distinguish between unhatched eggs and very early nestling deaths, we treated both as part of early partial brood loss in analyses. Banded nestlings that did not fledge comprised LPBL. We included only nests that produced at least one banded chick and at least one fledgling. For LPBL, we set a binary indicator to 0 if all banded nestlings fledged, and 1 if not. The sample size for EPBL was larger than for LPBL; LPBL was a subset of the EPBL dataset, including only those nests that had at least 2 chicks at banding (Supplementary Material Table S1, Table S2). We determined the clutch initiation date for each PBG by using the age of the oldest nestling at banding to estimate the hatch date and subtracting 11 days (based on Ligon 1970) as the date the first egg was laid. We converted clutch initiation date to the ordinal date.

Statistical Analyses

We evaluated early partial brood loss (EPBL) and late partial brood loss (LPBL) separately for each of the three study sites. Covariates included the number of males (i.e., breeder males and male helpers), number of females (i.e., breeder females and female helpers), number of floaters, clutch size, lay date, group density (measured as the size of the Thiessen polygon), adults per hectare, and year. We assessed collinearity using Pearson's correlation coefficients and removed one of the pairwise variables if the absolute value of the correlation was greater than 0.6. We checked for multicollinearity by examining the variance inflation factors (VIFs) for all variables. All variables with VIFs <10 were retained across all site-specific models to get our working global model (Supplementary Material Table S3; Dormann et al. 2013). At Lejeune, we observed strong correlation between adults per hectare and number of males with $r = 0.65$. Adults per hectare also exhibited a high VIF (>10). Therefore, we avoided including both predictors in the same model. We interpreted models with male count as capturing social group structure and those with adults per hectare as capturing breeder density, allowing us to maintain biological clarity while minimizing collinearity concerns.

We built 62 unique models to determine the relative effect of density metrics, group density and adults per hectare on the probability of occurrence of either EPBL or LPBL across all three sites. Each response variable was modeled as a logistic mixed-effects model using glmmTMB (Brooks et al. 2017) in R (R Core Team 2024). We constructed a priori models to include year and cluster ID as random effects, and lay date as a fixed effect (Table 1). Then we added different combinations of other covariates to create the model set. We ranked models using Akaike Information Criterion (AIC) and ΔAIC (Akaike 1973; Supplementary Material Table S4) and performed model averaging for models with a ΔAIC ≤ 2. We classified predictors as significant if their estimated 95% model-averaged confidence intervals did not overlap zero. We present the significant model-averaged predictors from each a priori model for EPBL and LPBL at each site (Figures 2 and 3).

Results

Group density decreased over time at Sandhills and increased at Lejeune and Eglin; adults per hectare increased at Sandhills, declined at Eglin, and showed an initial increase followed by a plateau at Lejeune (Figures 4 and 5). The occurrence of EPBL at Sandhills and Eglin showed non-linear trends over time. At Sandhills, EPBL declined from the late 1980s through the early 2000s but increased thereafter. At Eglin, the trend was relatively stable, with some evidence of an increase in more recent years. The occurrence of LPBL increased at both Sandhills and Eglin. EPBL and LPBL showed less consistent trends at Lejeune (Figures 6 and 7). LPBL increased significantly at Sandhills over the study period, while there was little evidence of temporal change in EPBL or LPBL at the other sites.

We tested for predictors of EPBL at Sandhills (n = 2,274 cluster-years, where a cluster-year represents one breeding group (cluster) observed in a single year), Lejeune (n = 1,502), and Eglin (n = 513), and LPBL at Sandhills (n = 1,903), LJ (n = 1,238), and Eglin (n = 370). EPBL models that included lay date received support for one of three sites while male count and clutch size received support for all three sites (Figure 2). LPBL models that included female count received support for one of three sites, lay date received support for one of three sites, year received support for one of three sites, and clutch size received support for two of three sites (Figure 3). Model averaged parameter estimates provided no evidence that the two measures of density, group density and adults per hectare, were related to EPBL or LPBL.

Model-averaged parameter estimates for EPBL indicated that as clutch size increased, the probability of EPBL increased at Sandhills (1.02, SE = 0.06), Lejeune (1.18, SE = 0.08) and Eglin (1.08, SE = 0.13). As lay date became later, the probability of EPBL increased at Sandhills (0.38, SE = 0.05), and as the number of males in the group increased the probability of EPBL decreased at Sandhills (-0.52, SE = 0.05), decreased at Lejeune (-0.45, SE = 0.07), and decreased at Eglin (-0.43, SE = 0.11; Supplementary Material Table S5).

Model-averaged parameter estimates for LPBL indicated that the probability of occurrence of LPBL increased as clutch size increased at Sandhills (0.24, se = 0.05) and Lejeune (0.25, se = 0.06). Over time (i.e., as year increased), the probability of occurrence of LPBL increased at Sandhills (0.29, se = 0.07), the probability of occurrence of LPBL increased for later lay dates at Sandhills (0.34, se = 0.05; Supplementary Material Table S5). As the number of females in a group increased, the probability of LPBL decreased at Eglin (-0.25, se = 0.11).

Discussion

Both measures of density — group density and adults per hectare – were unrelated to both EPBL and LPBL at all three study sites, indicating that partial brood loss in RCWs is not impacted by the number of neighboring groups or overall population density. This finding may result from the cooperative breeding system of RCWs. In non-cooperative species, increased density often intensifies competition for resources or nest sites, leading to reduced reproductive success, but the social structure of cooperative breeders may mitigate these effects by distributing care among multiple group members. Alternatively, this lack of relationship between population density and partial brood loss may be because RCW densities at our sites were below the threshold at which density-dependent effects emerge. Previous studies (e.g., Garabedian et al. 2018) have shown that negative effects of density on productivity are evident in RCWs at a particular density. Carrying capacity of our study populations is unknown, though two of the sites have now reached their recovery goals (within their original geographic extent). It may be that these populations remain well below carrying capacity, and that density-dependent processes could become more apparent as populations approach local carrying capacity. If this is the case, the densities for which RCWs are currently managed (USFWS 2003) may be well below what landscapes can support.

The probability of EPBL increased in nests with larger clutches and later lay dates, indicating that early-stage brood reduction may be linked to reproductive investment and limited group support. In contrast, LPBL also increased with clutch size at some sites but showed less consistent relationships with group composition (i.e., number of males and females) or lay date. Notably, LPBL increased over time at one site, while EPBL did not, indicating possible long-term shifts in late-stage reproductive outcomes.

The consistent effect of clutch size on EPBL across all three sites indicates that laying more eggs does not necessarily lead to higher reproductive output. Instead, larger clutches appear to increase the probability of brood reduction, particularly during the early nestling period. This pattern supports the brood reduction hypothesis (Lack 1947, O'Connor 1984), which posits that parents may overproduce offspring as a form of reproductive "insurance" in unpredictable environments. When resource availability or caregiving capacity is insufficient, some chicks may be lost — a cost potentially offset by the benefit of maximizing output under favorable conditions. This aligns with life-history and parental investment theory (Trivers 1972), which predict trade-offs between offspring quantity and quality. In cooperative breeders, these trade-offs may be further shaped by the number and contribution of helpers (Hatchwell 1999). Although we did not directly measure group or helper investments in parental care, our findings suggest that social dynamics could impose additional constraints on clutch size, particularly if helper capacity is limited or if competition for resources reduces the group's ability to support larger broods (Emlen 1982, Koenig and Dickinson 2004).

The effects of lay date on EPBL at Sandhills and on LPBL at Sandhills indicate that RCW nests initiated later in the season are less successful, likely due to environmental or social constraints. Later nests typically yield lower reproductive success in temperate bird species, largely because late nests occur after the seasonal peak in food availability, resulting in poorer feeding conditions for chicks (Lack 1954, Perrins 1970, Morbey & Ydenberg 2001, Verhulst & Nilsson 2008). In RCWs, however, this pattern indicates that later nests may still succeed partially, but at a cost to total fledging output. This interpretation is supported by DeMay and Walters (2019), who reported that earlier nesting and larger group sizes predicted higher productivity across 19 RCW populations. Environmental factors known to influence breeding phenology—such as temperature, precipitation, and vegetation conditions—likely contribute to these outcomes. Warmer early spring temperatures are associated with earlier nesting and increased productivity, whereas greater precipitation can delay breeding and reduce success (Fullerton et al. 2021). In addition, vegetation characteristics such as the presence of large pines and reduced hardwood midstory are linked to lower rates of partial brood loss, likely by improving foraging conditions prior to breeding (Martin et al. 2023).

The negative relationship between early partial brood loss (EPBL) and the number of males at all three sites supports long-standing evidence that larger social groups improve reproductive outcomes in cooperatively breeding species (Brown 1987; Emlen 1997; Mumme 1997). In RCWs, group size is a consistent predictor of reproductive success, with larger groups associated with increased fledgling production and nest survival (Lennartz et al. 1987; Walters & Garcia 2016; DeMay et al. 2019; Kappes et al. 2020). These benefits align with broader patterns in cooperative breeders, where helpers contribute to provisioning, defense, and cavity maintenance (Lloyd et al. 2009; Preston et al. 2016; Van de Loock 2017). Our findings—that EPBL is reduced in groups with more males—likely reflect the enhanced caregiving capacity provided by larger, male-rich groups.

In RCWs, the reproductive benefits of group size are largely driven by the presence of male helpers, who play a critical role in nestling care through food provisioning, cavity maintenance, and predator defense. Groups with one or more male helpers consistently fledge more offspring than those without (Khan & Walters 2002), underscoring that it is not only group size but also group composition that shapes reproductive outcomes. Helpers can have additive effects on nesting success by increasing the amount of food delivered to nestlings (Komdeur 1994; Doerr & Doerr 2007), especially in species prone to nestling starvation and brood reduction (Hatchwell 1999; Koenig & Walters 2011). Male helpers may alleviate the energetic demands placed on breeding males by sharing foraging and defense duties, allowing breeders to allocate more energy to offspring care and future reproduction (Heppell et al. 1994; Walters 1990).

Female helpers were significant predictors of reduced LPBL at only one site in our study, contrasting with findings by Kerr et al. (2024), who did not detect an effect of female helpers on partial brood loss. This discrepancy may stem from differences in how brood loss was measured; Kerr et al. combined early and late partial brood loss (EPBL and LPBL), potentially obscuring effects that emerge later in the nestling period, when female helper contributions may become more influential. Additionally, female helpers make up a much larger proportion of the helper pool at Eglin — where we observed this effect — indicating that demographic variation across sites may shape helper impacts.

Site-specific variation in the year effect on late partial brood loss (LPBL) between Sandhills, Lejeune, and Eglin suggests that temporal drivers of reproductive success—such as climate—may be more influential in some regions than others. Weather variability, including fluctuations in temperature and precipitation, can influence both nest initiation and partial brood loss in RCWs; interannual climate variation has been shown to affect nest initiation dates and overall reproductive success, highlighting the role of climate in shaping breeding outcomes (Fullerton et al. 2021). Notably, Sandhills is an inland site characterized by higher reproductive output but lower adult survival compared to the coastal sites Lejeune and Eglin. This pattern indicates that reproductive effort may be greater at Sandhills, potentially making reproduction more sensitive to climate variability at this site.

Future research that considers temporal and site-specific factors influencing reproductive success will advance knowledge about the drivers of partial brood loss in RCWs. Our analyses used a binary indicator of brood loss. While this binary approach minimized the risk of overinterpreting imprecise estimates, examining the proportion of offspring lost remains a valuable direction that could help clarify mechanisms of brood reduction. Future work incorporating more frequent monitoring could also help disentangle the proximate drivers of early losses. Beyond this, the interaction between group density and habitat quality—such as cavity availability, food abundance, or vegetation structure—may play a critical role in shaping reproductive outcomes. Habitat quality can mediate the impact of social factors like density by influencing the resources available to breeding groups, their space use, and their ability to provision offspring (Conner et al. 1999, Garabedian et al. 2018). Notably, the highest density areas—at least on Sandhills and Lejeune—also correspond to the areas of highest habitat quality (Walters, unpublished data), indicating that increased density does not necessarily imply reduced resource availability. Additionally, long-term changes in climate (e.g., temperature and rainfall patterns) or site-level disturbances (e.g., fire frequency, timber harvest) could affect lay dates and resource availability, further shaping patterns of reproductive success. Incorporating habitat quality and environmental variability into future studies may reveal context-dependent effects of density that were not detectable in the present analysis.

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Table 2.1. Independent and dependent variables used in the development of a priori early and late partial brood loss occurrence models for each site. Variables are annotated as follows: (†) denotes a fixed and random variable and (§) denotes a random effect only. Variables in italics indicate inclusion in working global model where VIFs<10.

Variable	Variable description
Year †	Year
Cluster §	Cluster ID
Lay Date	Estimated clutch initiation day
Clutch Size	Number of eggs
Male Count	Sum of breeder males and male helpers per cluster
Female Count	Sum of breeder females and female helpers per cluster
Floater Count	Total number of floaters per cluster

Total Adults	Sum of breeder males, breeder females, male helpers, and female helpers
Group Density	Total area (ha) per cluster
Adults per Hectare	Total adults divided by total area (ha)

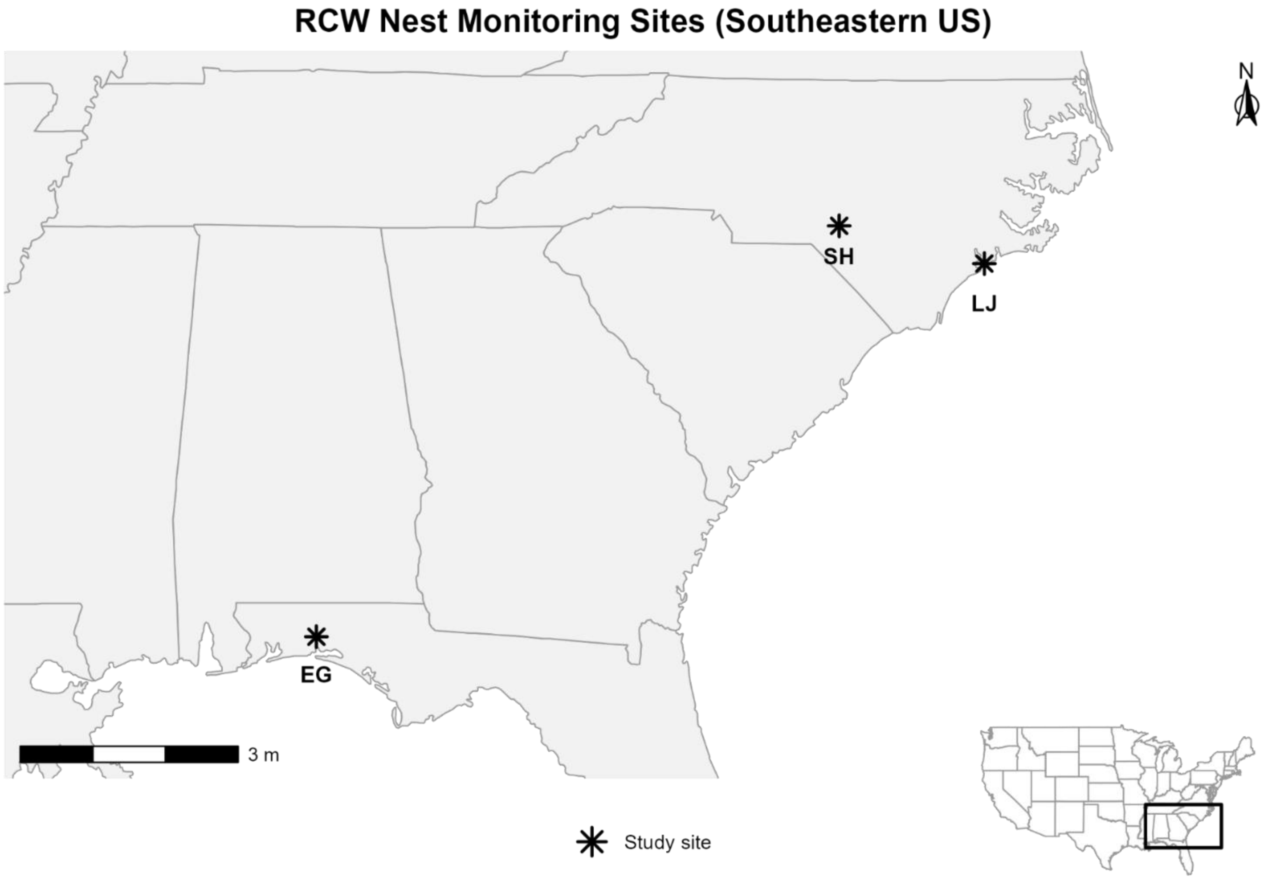

Figure 2.1. Location of the Sandhills , Lejeune , and Eglin study sites where we monitored Red-Cockaded Woodpecker (*Dryobates borealis*) reproduction from 1980 to 2023 in the southeastern United States.

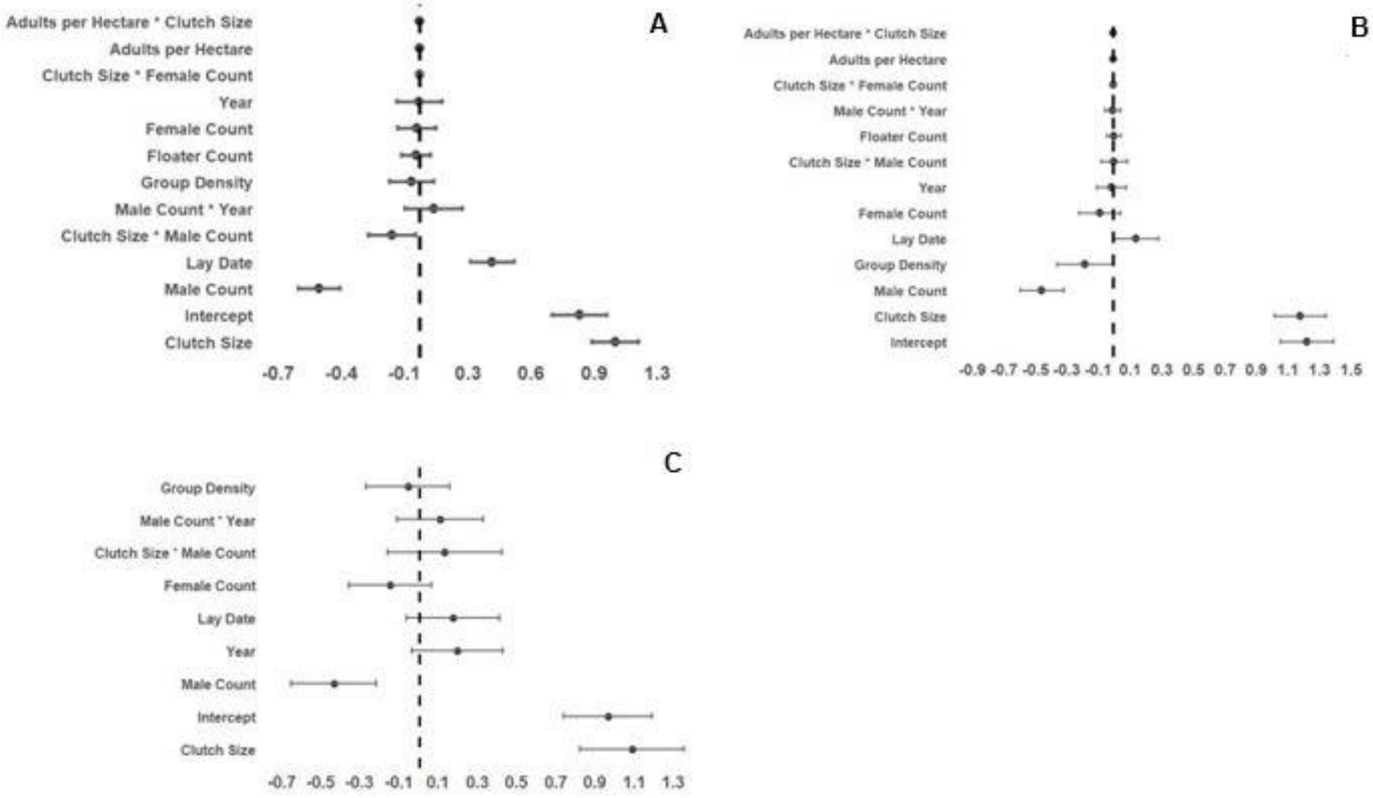

Figure 2.2. Model-averaged standardized coefficient plots for predictors influencing the occurrence of Early partial brood loss (EPBL) for the Sandhills (A) , Lejeune (B), and Eglin (C) study sites.

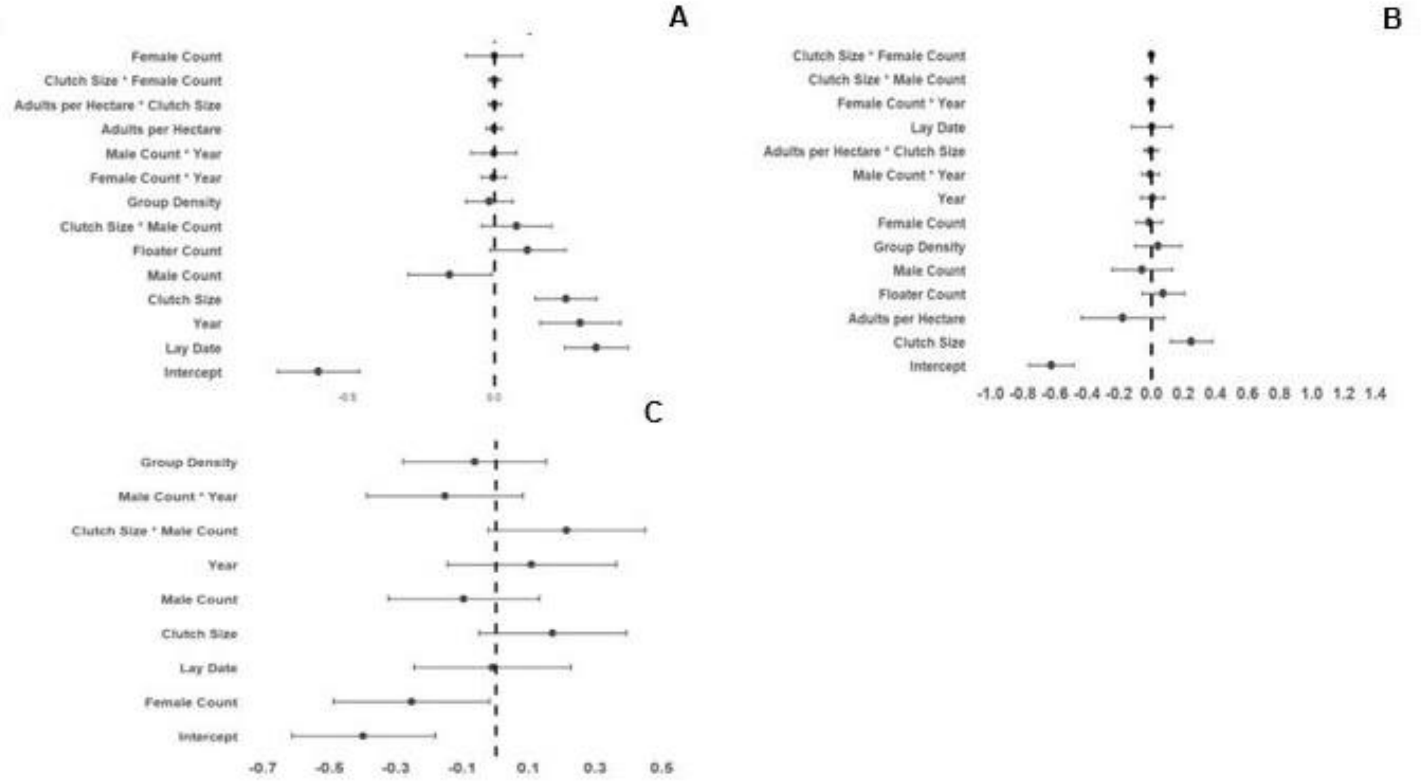

Figure 2.3. Model-averaged standardized coefficient plots for predictors influencing the occurrence of Late partial brood loss (LPBL) for the Sandhills (A), Lejeune (B), and Eglin (C) study sites. Each plot displays estimated effects of multiple predictors—such as clutch size, year, and various interaction terms—on reproductive outcomes, with black points representing effect sizes and horizontal lines showing 95% confidence intervals. A vertical dashed line at zero indicates the null effect threshold.

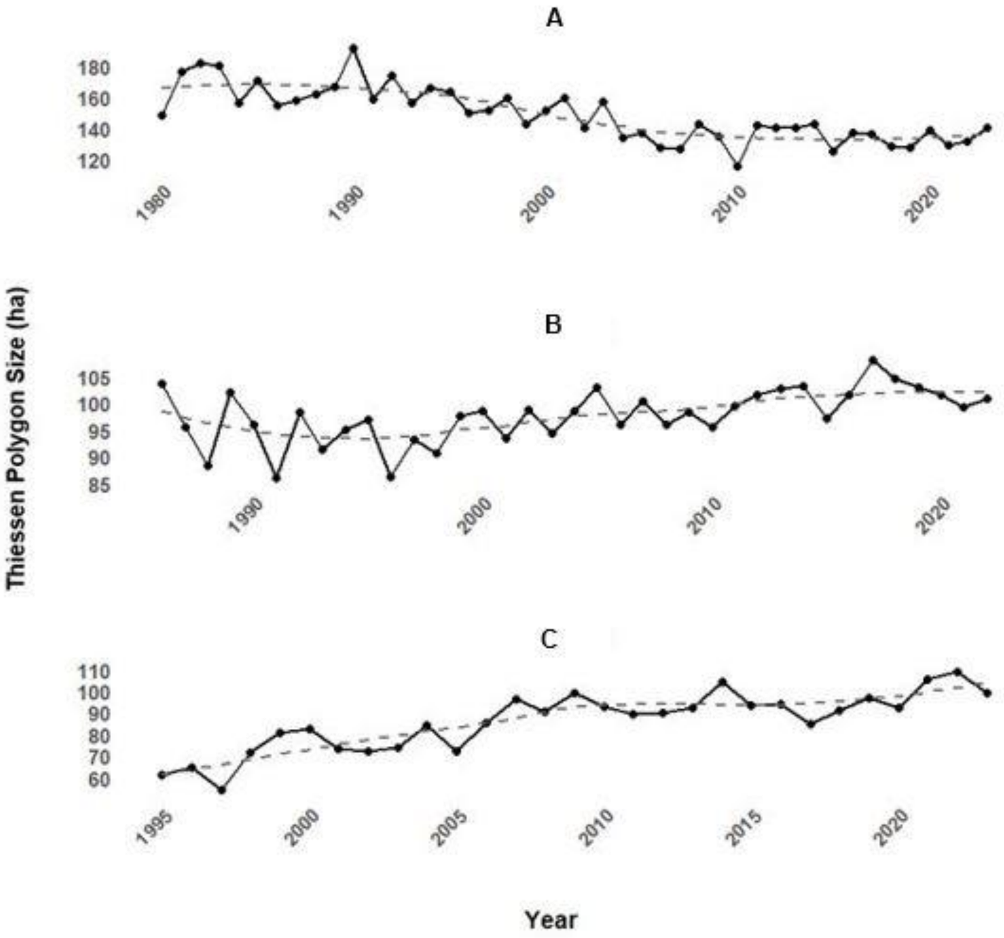

Figure 2.4. Temporal trends for group density (i.e., Thiessen polygon size) for the Sandhills (A), Lejeune (Lejeune), and Eglin (Eglin) study sites. The x-axis represents Year, and the y-axis represents Average group density (ha) with different ranges tailored to each site.

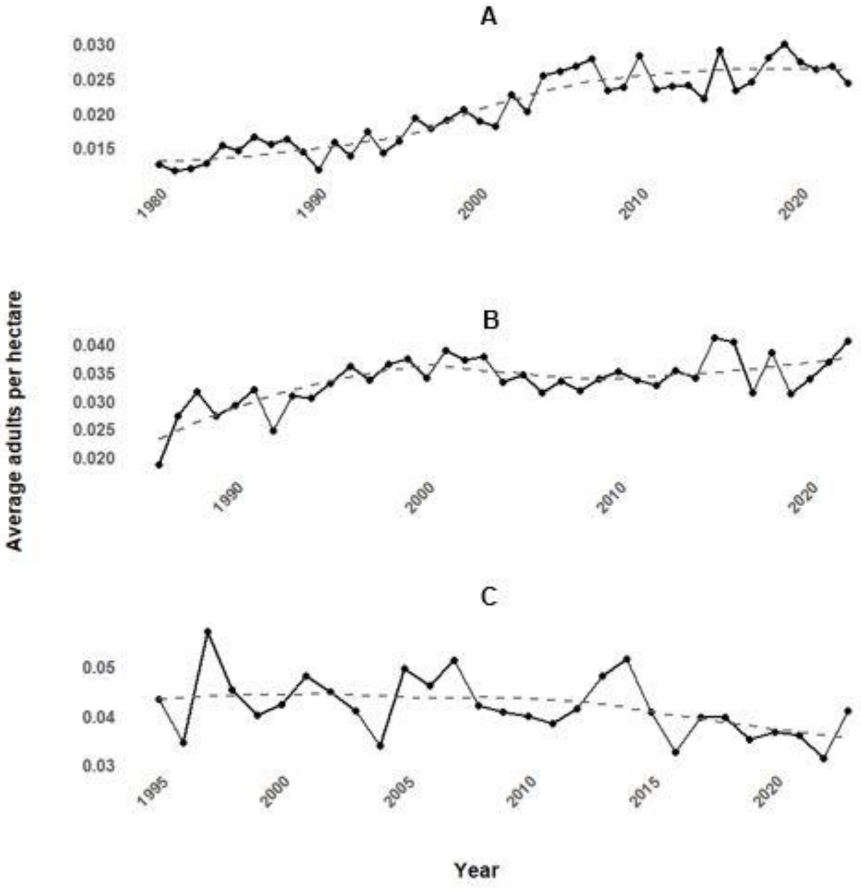

Figure 2.5. Temporal trends for average adults per hectare (i.e., number of adults divided by Theissen polygon size) for the Sandhills (A), Lejeune (B), and Eglin (C) study sites.

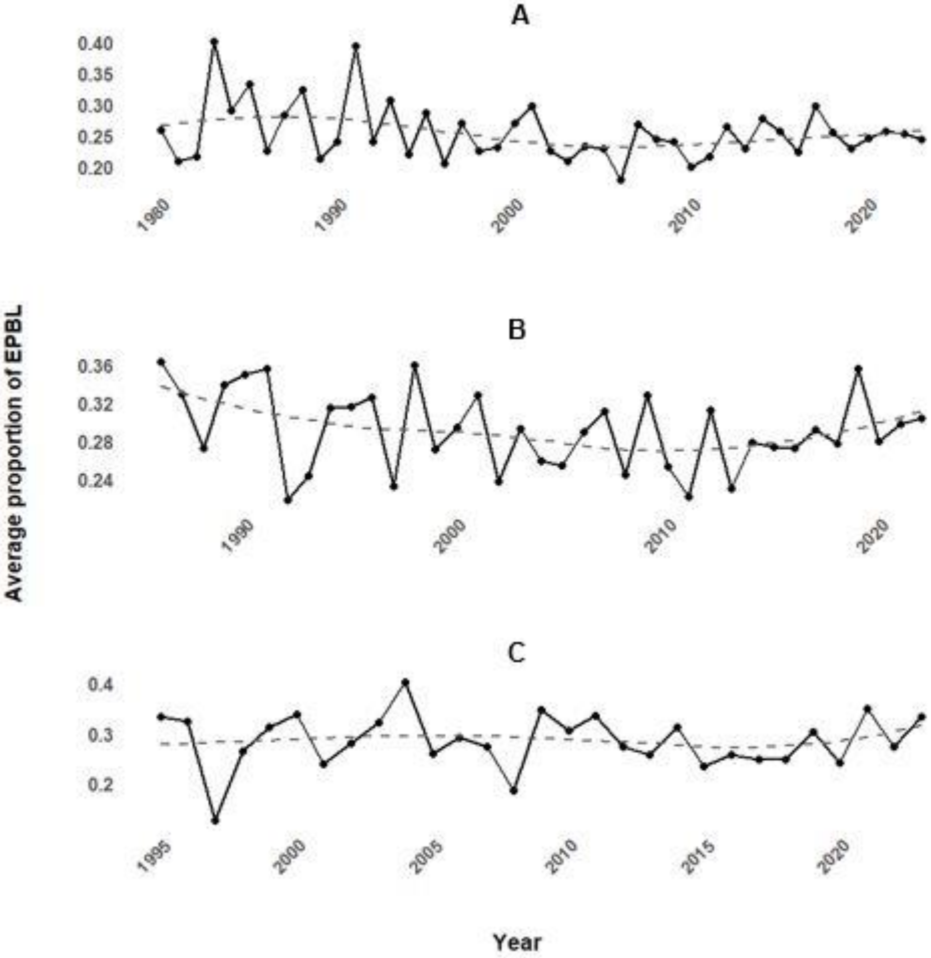

Figure 2.6. Temporal trends for the proportion of groups experiencing early partial brood loss (EPBL) for the Sandhills (A), Lejeune (B), and Eglin (C) study sites.

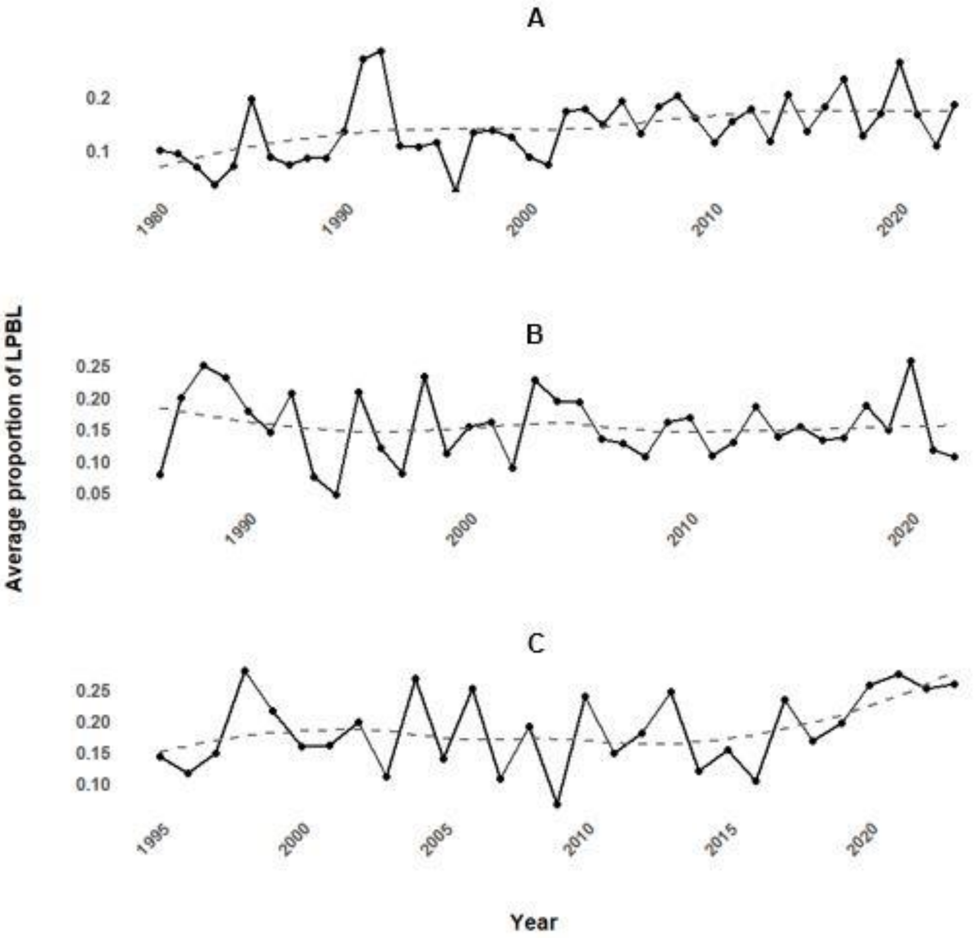

Figure 2.7. Temporal trends for the proportion of groups experiencing late partial brood loss (LPBL) for the Sandhills (A), Lejeune (B), and Eglin (C) study sites.

CHAPTER 3: WEATHER EFFECTS ON EARLY PARTIAL BROOD LOSS IN A THREATENED COOPERATIVE BREEDER

Pharr, L.D.; Cooper, C.B.; Moorman, C.E.; Hostetter, N.J.; Sorenson, C.E.; Walters, J.R.

Introduction

Climate warming has advanced laying dates in some birds (Parmesan 2003; Tøttrup et al. 2006). Earlier nest initiation can alter reproductive outcomes, including egg and brood loss (Adamík & Král 2008; Dunn et al. 2010; Wegge & Rolstad 2017). Air temperatures beyond species' physiological limits can cause direct nestling mortality through dehydration or rapid weight loss (Gebhardt-Henrich & Richner 1998; Lloyd & Martin 2004). Shifts in breeding phenology at individual and population scales are often interpreted as evidence of birds responding to spring temperatures as cues for nesting which historically produced broods at the time of peak food abundance; a pattern disrupted by climate change (Visser et al. 2004; Both et al. 2008). A consequence of early nesting induced by climate change can be increased chick mortality because brood-rearing precedes peak food availability (Ludwig et al. 2006; Dickey et al. 2008; Şekercioğlu et al. 2012).

Rising temperatures during the laying phase can shift the timing of incubation. Because embryos develop only above a species-specific physiological zero (≈ 26 °C / 78 °F), eggs exposed to warm conditions while untended may start and stop development or overheat, reducing hatchability through increased embryonic mortality (Stoleson & Beissinger 1999; Webb 1987; Deeming 2004). To limit these losses, parents may advance incubation—sometimes before clutch completion—which increases hatching asynchrony, intensifies within-brood competition, and can lead to greater partial brood loss (Wiebe & Bortolotti 1994; Clark & Wilson 1981).

These parental responses are shaped both by immediate weather at the nest and by nest microclimate (e.g., shade, cavity depth, exposure), and involve trade-offs between time spent incubating or brooding to regulate egg and chick temperatures versus time spent foraging to meet energetic demands (Deeming 2002; Conway & Martin 2000; Ardia et al. 2006; Wiebe 2001). In cooperative breeders, helpers can partially buffer these trade-offs by contributing to incubation or brooding and by increasing food delivery rates, which can reduce within-brood competition and lessen the likelihood that hatching asynchrony will result in partial brood loss (Hatchwell & Komdeur 2000; Koenig & Dickinson 2004; Russell et al. 2007). Temperatures during laying thus provide a useful context for interpreting variation in incubation behavior and partial brood loss across sites and breeding systems.

High temperatures can strongly influence early nestling survival, making the post-hatch period a particularly sensitive stage of reproduction. During the post-hatch period, nestlings are particularly vulnerable to high temperatures, as their limited thermoregulatory capacity means exposure to lethal thresholds (≈ 40 °C / 104 °F) can rapidly cause mortality if shading, ventilation, or brooding are insufficient (Webb 1987; Dawson et al. 2005). especially in the first week after hatching, when nestlings are least capable of self-regulation (Salaberria et al. 2014; Diehl et al. 2023). Short-term weather during both laying and post-hatch phases thus provides a critical context for interpreting variation in incubation timing, chick survival, and partial brood loss across sites and breeding systems.

Increased rainfall can reshape reproductive outcomes through several, sometimes opposing, pathways. Heavy or prolonged rain reduces foraging opportunities and nest visitation rates, slowing growth and increasing partial brood loss when wet spells extend across days (Öberg et al. 2015, Trapote et al. 2023). Storm rainfall can also raise the risk of flooded or persistently cold, damp nest microclimates (Maziarz et al. 2022). In cooperative systems, helpers may buffer shortfalls in provisioning or brooding during wet periods, but the strength of this buffer depends on group size and carer composition; meteorological conditions (rain, time since rain) also alter provisioning rates and within-group coordination (Koenig & Dickinson 2004, Wiley & Ridley 2016, Trapote et al. 2023). Conversely, in arid or strongly seasonal environments, well-timed rainfall pulses can boost prey availability and improve reproductive output when breeding aligns with resource peaks (Jetz et al. 2008).

Climate change may affect cooperatively breeding species in unique ways because their reproductive success is mediated by social structure. In cooperative breeding species, individuals beyond the breeding pair—often offspring from previous years—contribute to raising young, providing benefits such as increased provisioning, enhanced nest defense, and higher fledging success (Cockburn 1998; Koenig and Dickinson 2004). These benefits can buffer breeding pairs against environmental variability. However, climate-driven changes in resource availability or breeding phenology may disrupt group cohesion or reduce the effectiveness of helpers (Jetz and Rubenstein 2011), potentially weakening these social advantages. Moreover, as climatic conditions become more variable, the timing of helper availability and breeding needs may become increasingly mismatched (Koenig and Walters 2015). As a result, cooperative breeders may face compounded risks such as reduced reproductive success, lower survival of offspring, increased energetic costs, population declines over time, and loss of group stability, making them particularly vulnerable to the subtle and cascading effects of a changing climate. Prior research on climatic influences on cooperatively breeding species has focused on poleward or elevational expansions, with far less attention given to the southern limits of species' ranges, where populations may face increasing thermal and environmental constraints. As such, there is a pressing need to examine how populations at the southern edge of a species' range are responding, or failing to respond, to climatic pressures, especially relative to more northerly populations. Additionally, few studies have examined how changing climate impacts cooperative breeding species — from clutch initiation to brood success.

The Red-cockaded Woodpecker (Dryobates borealis; hereafter RCW), a cooperative breeding, cavity-nestling bird endemic to the longleaf pine (Pinus palustris) ecosystem of the southeastern United States, may be especially vulnerable to climate driven declines in reproduction. A changing climate—including increases in temperature, precipitation, and natural disturbance severity (e.g., hurricanes)—has been linked to shifts in key life history traits of RCWs, including earlier egg-laying dates and larger clutch sizes, which are correlated with local temperature and rainfall patterns (Engstrom et al. 1990, Conner et al. 2005, Schiegg et al. 2002, Garcia et al. 2014, DeMay et al. 2019, Louthan et al. 2021). Shifting spring weather associated with climate change may also contribute to the elevated rates of early partial brood loss observed in RCW populations (Garcia et al. 2014), a phenomenon where early-stage brood loss, encompassing eggs that fail to hatch and mortality of newly hatched chicks within the first few days (LaBranche and Walters 1994, DeLotelle et al. 2004). Partial brood loss is greater in RCWs than in other primary cavity-nesting species in the United States (LaBranche and Walters 1994). In RCWs, approximately 30–50% of eggs laid fail to produce fledglings, with most losses occurring early—through hatching failure or mortality during the first few days after hatching (LaBranche and Walters 1994; Schiegg et al. 2002). By contrast, other primary cavity-nesting species such as red-bellied woodpeckers (Melanerpes carolinus), downy woodpeckers (Dryobates pubescens), and northern flickers (Colaptes auratus) typically experience much lower rates of partial brood loss, often below 10–15%, and most losses occur later in the nestling period rather than at the egg or very early nestling stage (Wiebe 2001; Martin and Li 1992). This pattern suggests that RCWs may be particularly vulnerable to environmental conditions during the earliest stages of reproduction. Notably, RCWs generally initiate incubation with the laying of the first egg, resulting in asynchronous hatching and prolonged exposure of early eggs and nestlings to ambient conditions (Ligon 1970; USFWS 2003; Martin et al. 2023). In addition, RCWs have an unusually long brood-rearing period—nestlings remain in the cavity for about 26–29 days before fledging, compared to roughly 10–14 days in many other small passerines—further extending the duration over which developing young are exposed to environmental stressors. Hence, it's important to determine how possible earlier clutch initiation dates interact with shifting weather conditions to affect early reproductive outcomes such as hatching success and early partial brood loss.

We analyzed the influence of climate change on early partial brood loss over a long timescale in three RCW populations. Climate change has been linked to shifts in egg-laying dates (Schiegg et al. 2002), with earlier laying and larger clutches correlated with local temperature and rainfall (Garcia et al. 2014). However, recent findings showed that increased rates of partial brood loss were not density dependent—that is, they were not associated with higher densities resulting from species recovery within limited longleaf habitats (Pharr et al. 2025). Building on this, we aimed to assess whether temperature and precipitation influence reproductive outcomes across multiple recovered RCW populations. Specifically, we evaluated how clutch initiation dates alter the temperature and precipitation conditions experienced by clutches during key phases of the breeding cycle, and whether variation in these weather conditions during laying, incubation, and early brood rearing predicts the likelihood of early partial brood loss. We assessed early partial brood loss at the level of individual eggs by modeling the per-egg probability of hatching failure or early nestling mortality as a function of site-specific weather conditions. We predicted that (1) early partial brood loss would increase during the laying period when maximum daily temperatures exceed physiological thresholds, (2) early partial brood loss during incubation and the post-hatch period would increase with higher maximum temperatures, and (3) the probability of early partial brood loss during the post-hatch period would increase with greater rainfall.

Materials and Methods

We acquired banding, group composition, and reproduction data from three RCW populations: (1) an inland site in the North Carolina Sandhills (1981–2023; 813 potential breeding groups (PBGs), (2) a site on the central coast of North Carolina at Marine Corps Base Camp Lejeune (1986–2022; 136 PBGs), and (3) a Gulf Coast Florida panhandle site at Eglin Air Force Base (1995–2023; 533 PBGs; Figure 1). Monitoring of individual RCW groups was facilitated by the conspicuous resin-coated cavities excavated in living pines and by the long-term stability of territories. Each territory in the study areas was visited prior to each breeding season to determine whether it was occupied, indicated by the presence of at least one active cavity tree. Thereafter, cavities were inspected within each active territory every 7-11 days to detect and monitor reproductive attempts. At 5-10 days post hatching, nestlings were banded with a unique combination of color bands. Groups were followed post-fledging to determine the identity and sex (based on sexually dimorphic crown patches) of fledged young. Color-banded adults were identified to obtain group size and composition, and each individual was assigned a status (e.g., breeder, floater, or helper) based on behavioral observations and their age. Unbanded adults immigrating into the study areas were captured from their roost trees and color banded.

Refer to Walters et al. (1988) for a more detailed description of data collection. We were only able to include years where complete data were available; thus, the site-years included in the analysis were variable based on the year data collection started for each site, with each site being analyzed separately for this analysis.

For each PBG, we included data on all nest attempts, clutch size, and number of nestlings. We defined early partial brood loss as the proportion of eggs that did not hatch into nestlings and nestlings that died before banding. Nests with a single egg were excluded because it is not possible to distinguish between whole brood loss and partial brood loss. Nests with more than five eggs were also excluded, as they are uncommon and typically result from co-breeding females. Additionally, only nests that successfully hatched at least one chick were included in the analysis (Supplementary Material Table S1). We included nest attempts in which pairs initiated one or two nesting attempts per breeding season. The estimated clutch initiation date for each PBG was determined by using the age of the oldest nestling at banding to estimate the hatch date and subtracting 11 days (based on Ligon 1970) to determine the date the first egg was laid. Clutch initiation dates were converted to ordinal dates for consistency. We examined patterns in per-egg probability of hatching failure, using each egg's failure (yes/no) as a binomial variable for all of our formal statistical analyses. We accounted for non-independence by using a unique identifier of each nest as a random-effect variable in statistical analyses.

Weather Data and Breeding Phenology

We used weather data from 1981 to 2023 to examine how annual variation in temperature and precipitation during the breeding season influenced key phases of the reproductive cycle. We obtained gridded daily maximum and minimum temperature and total precipitation data at a 4-

km spatial resolution—the finest available for the geographic and temporal extent of our study—from PRISM (PRISM Climate Group, 2023).

To assess whether breeding phenology in RCWs has shifted over time, we examined long-term variation in clutch initiation dates across the three sites: Sandhills (1981–2023), Lejeune (1986–2022), and Eglin (1995–2023). For each nest, we estimated the date the first egg was laid and summarized annual distributions of clutch initiation dates (Figure 2). To place these phenological patterns in environmental context, we also extracted maximum and minimum daily temperatures corresponding to lay dates and summarized their distributions annually. This allowed us to evaluate both temporal consistency in laying phenology and the range of thermal environments under which reproduction occurred.

To capture conditions experienced during early brood rearing from April to May of the breeding year for each nest location, we calculated the average daily maximum temperature (°F), and average daily precipitation (inches) during three biologically relevant phases: (1) the laying period, defined as the span of egg laying prior to the onset of full incubation; (2) the incubation period, defined as the time after laying is complete and until first egg hatches.; and (3) the post-hatch period, defined as the 8 days after the first egg hatched. Additionally, we calculated the percent of days exceeding physiological zero (>78.8°F) during the laying phase to assess exposure to temperatures above physiological zero, which may affect egg viability. For incubation and post-hatch phases, we used average daily maximum temperatures. Extreme heat days (>104.9°F) were rare and provided limited variation.

Statistical Analyses

We evaluated the per-egg probability separately for each of the three sites. In addition to weather covariates, we included covariates that were statistically significant and site-specific as predictors of early partial brood loss, based on results from Pharr et al. (2025). Models for Sandhills, Lejeune, and Eglin incorporated the number of males in the group (breeders plus helpers) and clutch size as covariates; lay date was additionally included for Sandhills. Weather covariates were percent laying days above 78.8°F, average laying period daily precipitation, average incubation daily maximum temperature, average incubation daily precipitation, average post-hatch daily maximum temperature, and average post-hatch daily precipitation. We assessed collinearity using Pearson's correlation coefficients; no variables were removed. We checked for multicollinearity by examining the variance inflation factors (VIFs) for all variables (Supplementary Material Table S2). All variables with VIFs <10 were retained across all site-specific models to yield a global model (Dormann et al. 2013).

We built five unique models to determine the relative effect of weather on per egg hatching probability across all three sites. Each response variable was modeled as a logistic mixed-effects model using glmmTMB (Brooks et al. 2017) in R (R Core Team 2024). We constructed *a priori* models to include year, cluster ID, and clutch ID as random effects (Table 1). We used Akaike's information criterion (AIC; Akaike 1973) to select the best model among a set of biologically plausible candidate models. We selected the model with the smallest ΔAICc as the best among all models being compared (Supplementary Material Table S3). We classified predictors as significant if their estimated 95% confidence intervals did not overlap zero.

Results

Across sites, birds experienced a broad range of thermal environments during reproduction. At Sandhills (n = 6,290 eggs from 1,771 nests), laying-phase conditions exceeded the 78.8°F threshold on more than half of days observed (3,299 of 6,039 days; 54.6%). During incubation at Sandhills, maximum daily temperatures averaged 79.4°F (range 48.6–98.4°F;

13,933 days observed), and during the post-hatch phase, maximum daily temperatures averaged 80.9°F (range 49.3–98.5°F; 12,793 days observed). No incubation or post-hatch days exceeded the extreme heat threshold of 104.9°F at Sandhills. At Lejeune (n = 4,873 eggs from 1,354 nests), laying-phase conditions were generally cooler, with only 28.0% of days (1,358 of 4,852) exceeding 78.8°F. Incubation conditions averaged 76.7°F (range 61.9–92.4°F; 8,242 days observed), and post-hatch conditions averaged 77.9°F (range 59.1–97.6°F; 6,780 days observed), with no days surpassing 104.9°F at Lejeune. At Eglin (n = 1,772 eggs from 549 nests), laying-phase conditions were the warmest, with 78.4% of days (742 of 947) exceeding 78.8°F. Incubation temperatures averaged 83.2°F (5,338 days observed) and post-hatch temperatures averaged 84.9°F (4,356 days observed), with no days exceeding 104.9°F at Lejeune.

We tested for predictors of early partial brood loss at Sandhills (n = 1,771 cluster-years, where a cluster-year represents one breeding group observed in a single year), Lejuene (n = 1,354), and Eglin (n = 332). Nest attempt was a predictor of early partial brood loss at one of three sites, male count was a predictor at two of three sites, and clutch size was a predictor at all three sites (Figure 3). The occurrence of second nest attempts increased the probability of early partial brood loss at Sandhills (0.03, SE = 0.00). As clutch size increased, the probability of early partial brood loss increased at Sandhills (0.05, SE = 0.00), Lejeune (0.06, SE = 0.00) and Eglin (0.07, SE = 0.01), and as the number of males in the group increased the probability of early partial brood loss decreased at Sandhills (-0.05, SE = 0.00) and decreased at Lejeune (-0.04, SE = 0.00; Supplementary Material Table S4).

For weather variables, only average post-hatch daily maximum temperatures was related to early partial brood loss and only at one site, indicating that early partial brood loss increased as the post-hatch maximum temperature increased at Sandhills. As average post-hatch maximum temperatures increased, the probability of early partial brood loss increased at SH (0.01, SE = 0.00).

Discussion

Across sites, RCWs bred under a wide range of thermal environments, with Sandhills and Eglin experiencing more frequent high temperatures than Lejeune. Despite this variation, extreme heat events were absent, and early partial brood loss was affected by only one weather variable and only at one site. At Sandhills, elevated post-hatch maximum temperatures and later nesting attempts led to increased partial brood loss, highlighting localized sensitivity to thermal stress and seasonal constraints. At all three sites, larger clutches increased the likelihood of brood loss, whereas greater number of male helpers reduced brood loss at two sites pointing to the importance of group composition in buffering environmental stress. Our results demonstrate that cooperative breeding helps mitigate some environmental pressures by distributing care among group members, particularly under challenging thermal conditions, but that such buffering is not absolute and may be overwhelmed under certain site-specific or seasonal contexts.

The probability of early partial brood loss increased in nests experiencing higher average post-hatch temperatures at Sandhills, North Carolina, indicating site-specific sensitivity of nestlings to thermal stress. Elevated temperatures can directly impair nestling growth and survival (Andreasson et al., 2018; Rodríguez & Barba, 2016) and reduce parental provisioning (Wiley & Ridley, 2016). The absence of a relationship between early partial brood loss and temperature at other sites indicates that local environmental conditions may mediate vulnerability, consistent with evidence that thermal thresholds interact with ecological context to shape reproductive outcomes (Andrew et al., 2017; Cunningham et al., 2013).

Early partial brood loss increased in second nest attempts at the Sandhills study site, possibly because late nests may expose broods to resource limitations and heightened thermal stress. Later nest attempts often coincide with reduced food availability and hotter conditions, factors known to decrease nestling survival and parental provisioning efficiency (Verhulst & Nilsson, 2008; Verboven & Visser, 1998; Wiley & Ridley, 2016). The higher incidence of early partial brood loss in later nesting attempts underscores how timing within the breeding season interacts with weather to shape reproductive outcomes, and highlights the potential for climate change to amplify risks associated with delayed or repeat nesting attempts (Andrew et al., 2017; Cunningham et al., 2013).

The greater prevalence of early partial brood loss for larger clutches across all three sites indicates that laying more eggs does not necessarily lead to greater reproductive output. This relationship between clutch size and early brood loss supports the brood reduction hypothesis (Lack 1947, O'Connor 1984), which posits that parents may overproduce offspring as a form of reproductive "insurance" in unpredictable environments. When resource availability or caregiving capacity is insufficient, some chicks may be lost — a cost potentially offset by the benefit of maximizing output under favorable conditions. This aligns with life-history and parental investment theory (Trivers 1972), which predict trade-offs between offspring quantity and quality. In cooperative breeders, these trade-offs may be further shaped by the number and contribution of helpers (Hatchwell 1999). Although we did not directly measure group or helper investments in parental care, our results indicate that social dynamics could impose additional constraints on clutch size, particularly if helper capacity is limited or if competition for resources reduces the group's ability to support larger broods (Emlen 1982, Koenig and Dickinson 2004).

The negative relationship between early partial brood loss and the number of males at two of three sites supports earlier findings that larger, male-rich groups improve reproductive outcomes in RCWs (Pharr et al. 2025). Although Pharr et. al (2025) demonstrated this effect at the brood level, this study showed that these benefits also extend to the egg level, where groups with more male helpers experienced reduced early brood loss. The reduction in brood loss with an increased number of male helpers is consistent with long-standing evidence that male helpers enhance reproductive success in cooperatively breeding species by contributing to provisioning, defense, and cavity maintenance (Brown 1987; Emlen 1997; Mumme 1997; Khan & Walters 2002).

There are several possible explanations for why we detected no relationship between weather and early partial brood loss at Lejeune or Eglin. At Lejeune, temperatures were generally lower than at the other sites and fewer days exceeded the 78.8°F threshold, reducing the likelihood of heat stress effects on nestlings (Cunningham et al., 2013). At Eglin, temperatures were consistently high but less variable, which may have masked relationships with brood loss if birds are adapted to persistently warm conditions (Andrew et al., 2017). Site-specific environmental characteristics such as forest structure and prey availability may buffer thermal stress by moderating microclimates and sustaining provisioning rates (Dawson & Lawrie, 2019; Wiley & Ridley, 2016). Finally, cooperative group dynamics may help mitigate stress related to extreme weather and climate warming, with helpers compensating for reduced parental activity during hot conditions (Cockburn, 1998; Koenig & Dickinson, 2016). Together, these possibilities highlight the importance of local ecological context in mediating weather effects on reproductive outcomes and indicate that RCW populations may vary in their vulnerability to climate change.

Future research should build on these findings by disentangling the mechanisms through which weather and site-specific conditions influence reproductive outcomes in RCWs, particularly by examining how variation in group size and composition modulates resilience to environmental stress. Our results show that while additional male helpers may mitigate some of the costs of thermal stress or later-season breeding, these buffers are not absolute and can be overwhelmed under certain conditions, such as elevated post-hatch temperatures at Sandhills. Examining the mechanisms of this buffering—whether through increased provisioning or flexibility in parental care—would provide important insights into how cooperative groups cope with climate variability. Long-term monitoring of nestling growth and physiological condition in relation to group composition and weather could clarify how environmental stress translates into partial brood loss. As climate change intensifies, such studies will be essential for predicting whether cooperative breeding can continue to stabilize reproductive success or whether local vulnerabilities will lead to uneven outcomes across populations.

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Table 3.1. Independent and dependent variables used in the development climatic influence on the outcome of early partial brood loss models for each site. Variables are annotated as follows: (‡) denotes a dependent variable and (§) denotes a random effect only.

Variable	Variable description
Year §	Year
Clutch ID §	Combined Cluster ID, Year, and Attempt Group
Cluster ID §	Combined Cluster ID and Year
Per Egg Probability ‡	Binary outcome for egg hatch success (0) or failure (1)
Lay Date	Lay Dateed clutch initiation day
Clutch Size	Number of eggs
Male Count	Sum of breeder male and male helpers per cluster
Nest Attempt	The number of nest attempts per cluster per year

Percent Laying Days above 78.8	Percent of lay dates above 78.8 (°F) before full incubation. Spatial resolution: 4 km.
Average Laying Precipitation	Average Laying Precipitation (inch) of lay dates before full incubation. Spatial resolution: 4 km.
Average Incubation Maximum Temperature	Average Maximum Temperature (°F) of Incubation days. Spatial resolution: 4 km.
Average Incubation Precipitation	Average incubation precipitation (inches) of Incubation days. Spatial resolution: 4 km.
Average Post-Hatch Maximum Temperature	Average Maximum Temperature (°F) of post-hatch days. Spatial resolution: 4 km.
Average Post-Hatch Precipitation	Average precipitation (inches) of post-

hatch days. Spatial
resolution: 4 km.

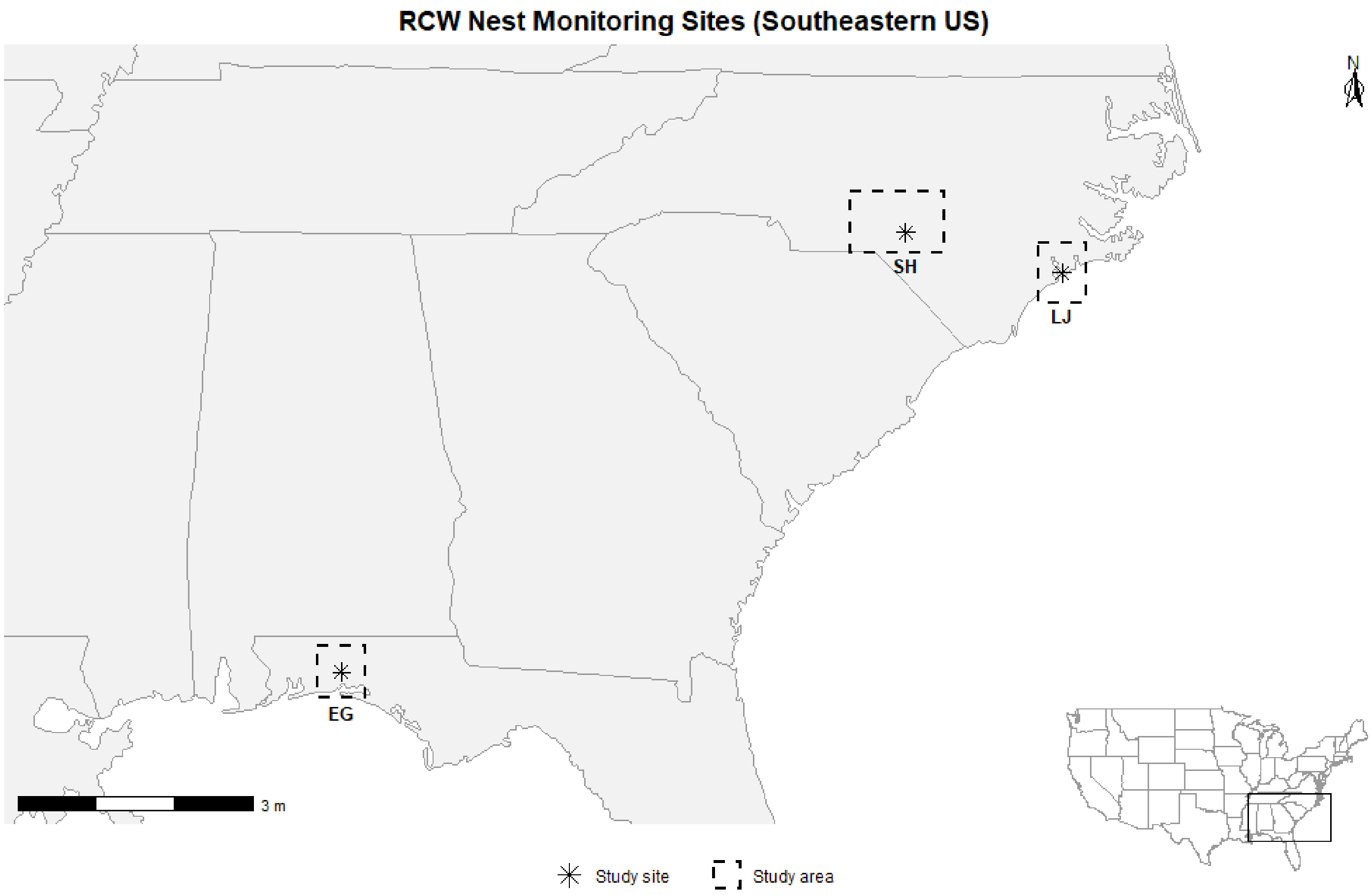

Figure 3.1. Location of the Sandhills, Lejeune, and Eglin sites where we monitored red cockaded woodpecker (*Dryobates borealis*) reproduction from 1981 to 2023 in the southeastern U.S.

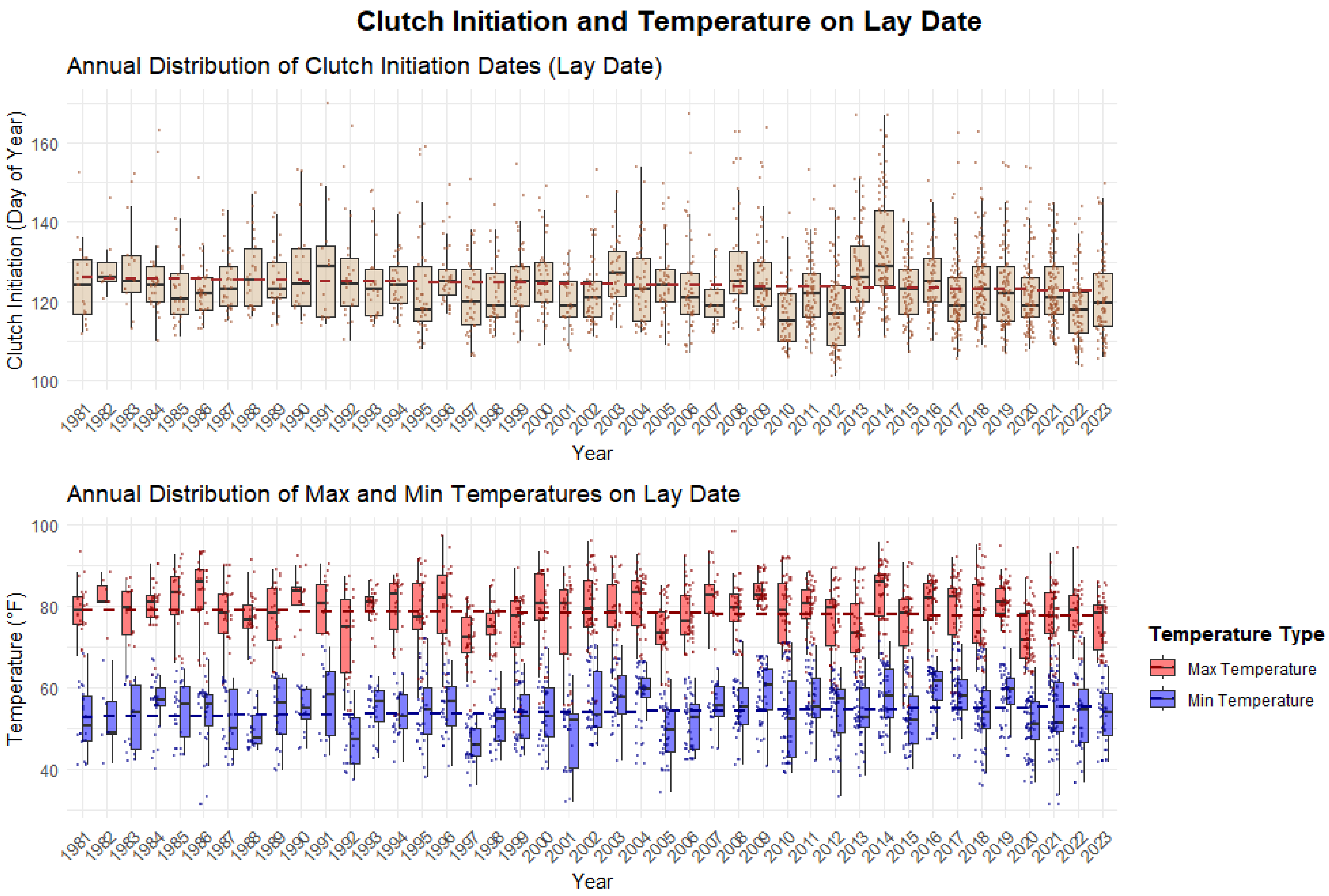

Figure 3.2. Annual distribution of year-specific variation of clutch initiation dates (lay dates, top panel) and corresponding maximum and minimum daily temperatures on lay dates (bottom panel) for Sandhills (1981-2023). Temperature distributions are separated by type: maximum (red) and minimum (blue) temperatures on the day the first egg was laid in each nest.

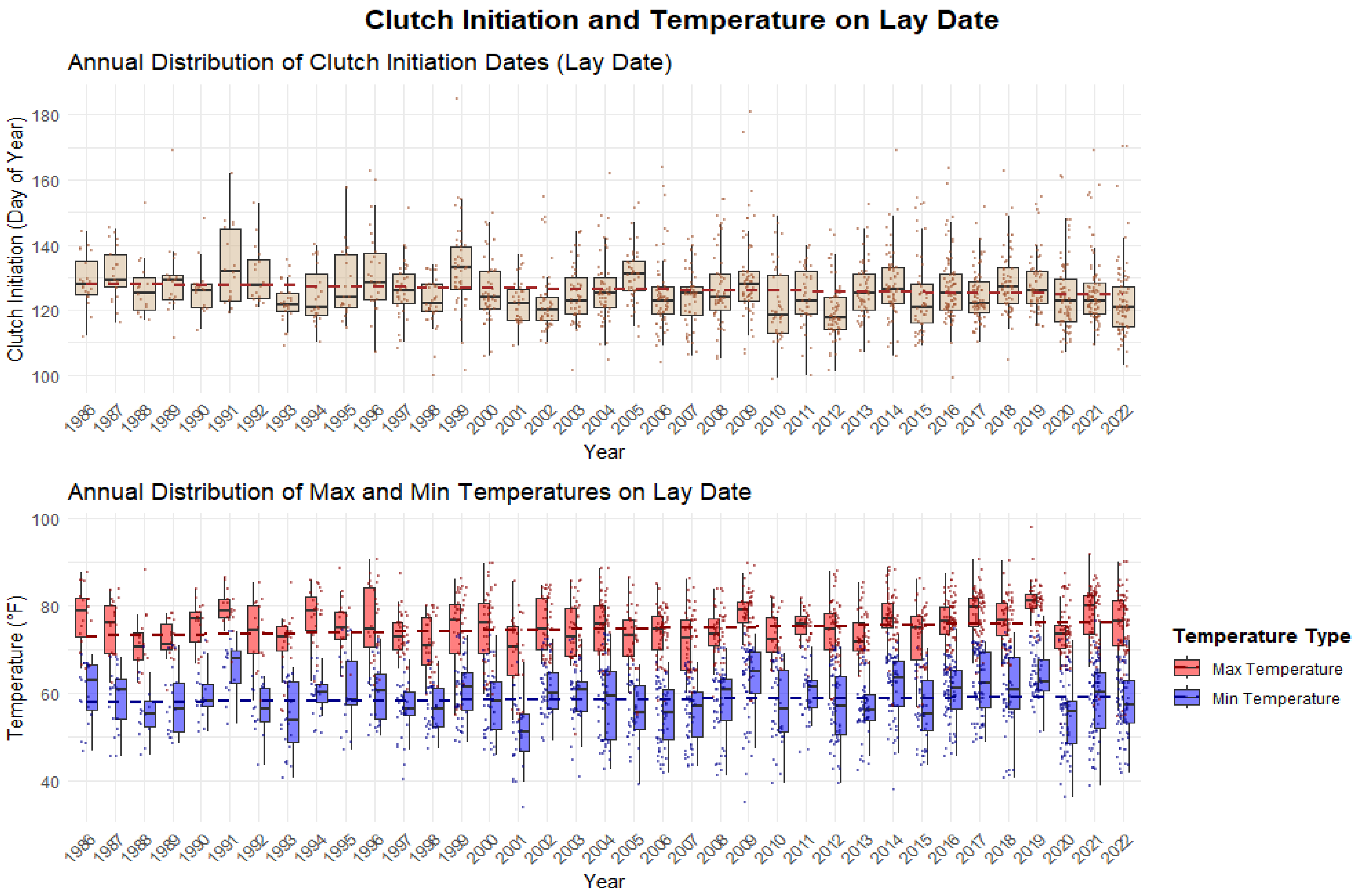

Figure 3.3. Annual distribution of year-specific variation of clutch initiation dates (lay dates, top panel) and corresponding maximum and minimum daily temperatures on lay dates (bottom panel) for Lejeune (1986-2022). Temperature distributions are separated by type: maximum (red) and minimum (blue) temperatures on the day the first egg was laid in each nest.

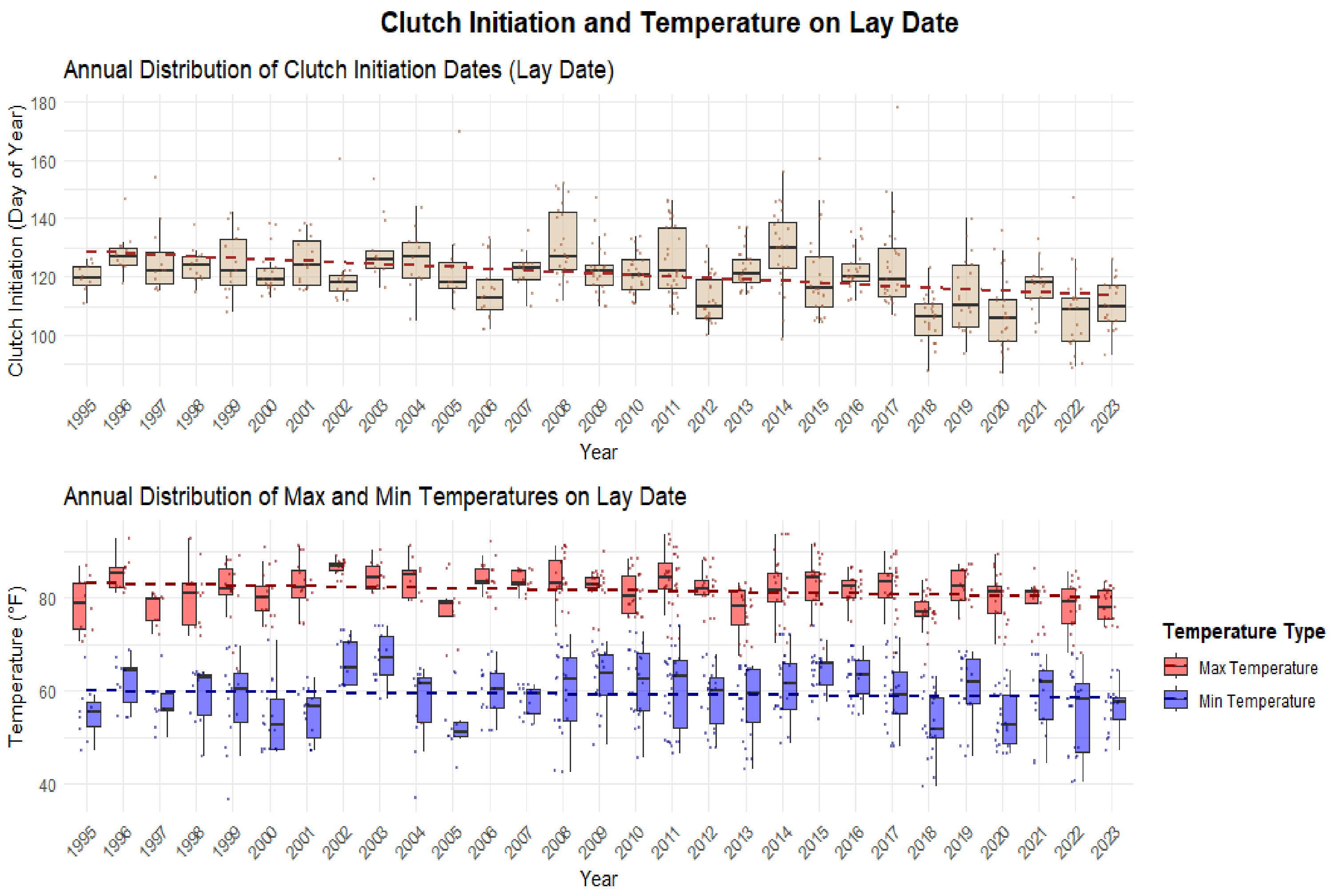

Figure 3.4. Annual distribution of year-specific variation of clutch initiation dates (lay dates, top panel) and corresponding maximum and minimum daily temperatures on lay dates (bottom panel) for Eglin (1995-2023). Temperature distributions are separated by type: maximum (red) and minimum (blue) temperatures on the day the first egg was laid in each nest.

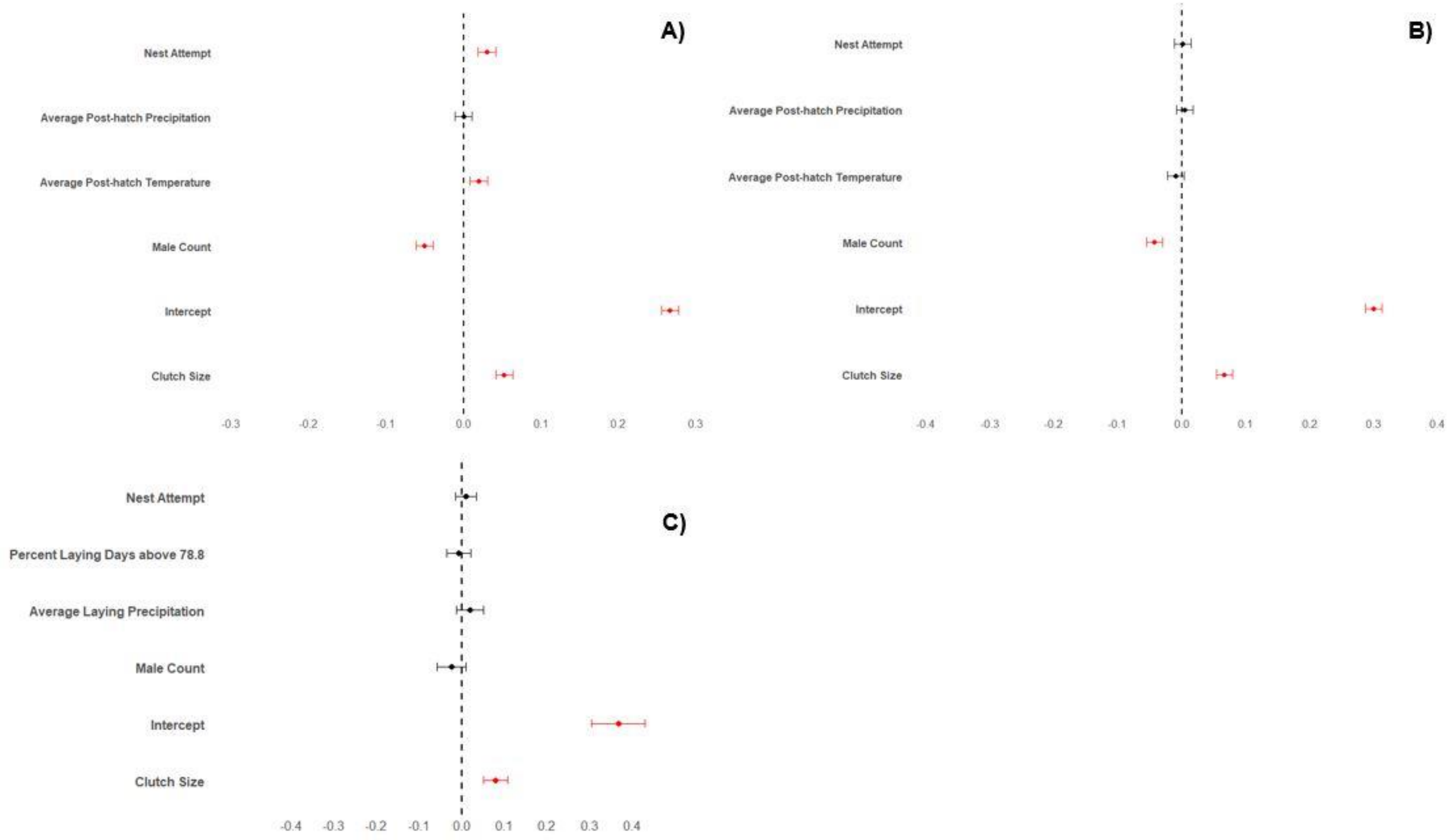

Figure 3.5. Standardized coefficient plots for predictors for climatic influence on the occurrence of early partial brood loss at Sandhills (A), Lejeune (B), and Eglin (C) study site.

CHAPTER 4: INFLUENCE OF CHICK SIZE AND WEATHER ON LATE PARTIAL BROOD LOSS IN A THREATENED COOPERATIVE BREEDER

Pharr, L.D.; Cooper, C.B.; Moorman, C.E.; Hostetter, N.J.; Sorenson, C.E.; Walters, J.R.

Introduction

Partial brood loss—the death of one or more nestlings before fledging—is a widespread and ecologically important source of reproductive failure in altricial birds (Mock & Parker 1997; Stoleson & Beissinger 1995). Because only a subset of chicks survive, partial brood loss directly constrains population productivity and can shape parental reproductive strategies. Brood loss typically occurs when competitive hierarchies develop within broods, placing smaller, lower-ranked nestlings at greater risk of starvation, neglect, or competitive exclusion. These size hierarchies can arise through multiple pathways, including hatching asynchrony (when incubation begins before clutch completion and eggs hatch on staggered schedules; Stenning 1996; Magrath 1990; Forbes & Glassey 2000), but can also be amplified or mitigated by environmental and social conditions that shape nestling growth trajectories and parental care.

A substantial body of theory has sought to explain the evolutionary basis of size hierarchies and brood reduction. The brood-reduction hypothesis proposes that parents may tolerate or promote hierarchies to ensure that at least one chick survives if food becomes scarce (Lack 1968). The nest-failure or insurance hypotheses suggest that initiating incubation early may help ensure that at least one chick survives if the nest fails due to predation or disturbance (Hussell 1972; Clark & Wilson 1981). Other perspectives emphasize that early incubation may serve to protect egg viability, as prolonged exposure to ambient conditions can reduce hatchability (Arnold et al. 1987; Ewert 1992). Although these hypotheses differ, they converge on the idea that environmental variation can strongly influence chick survival by shaping the degree of size inequality within broods—and thus the risk of partial brood loss. Alternatively, some have argued that size hierarchies arise not from adaptive strategies but as incidental byproducts of behavioral or physiological constraints on incubation timing (Amundsen & Stokland 1988; Slagsvold & Lifjeld 1989; Table 1). For example, one such constraint arises when rising temperatures during the laying phase alter the onset of incubation. Because embryos develop only above a species-specific physiological zero (≈26 °C / 78 °F), eggs exposed to warm conditions while untended may start and stop development or overheat, thereby reducing hatchability through increased embryonic mortality (Stoleson & Beissinger 1999; Webb 1987; Deeming 2004).

Environmental conditions are especially likely to affect the dynamics related to partial brood loss because they act at multiple stages of reproduction. During laying, warmer ambient temperatures can accelerate embryo development in early-laid eggs, leading to larger size hierarchies once hatching occurs. During brood-rearing, both temperature and precipitation can influence food availability, alter foraging efficiency, or modify nest microclimate, with hot or wet conditions increasing energetic stress and disproportionately affecting smaller nestlings. These processes intensify competitive asymmetries within broods, raising the likelihood that the smallest chicks will die. Social factors—including the number of provisioning adults—can further influence the degree to which size hierarchies develop and whether they result in brood reduction. Yet, despite this extensive theoretical and empirical foundation, most studies have examined environmental and social influences separately, and relatively few have connected them together to show how they shape within-brood size variation and the likelihood of partial brood loss (e.g., Brouwer et al. 2006; Ridley & Raihani 2007; Raihani & Ridley 2008).

The Red-cockaded Woodpecker (*Dryobates borealis*; hereafter RCW) provides an ideal system for examining these processes. RCWs are a federally threatened, cooperatively breeding, cavity-nesting species endemic to the fire-maintained longleaf pine (Pinus palustris) ecosystem of the southeastern United States. Breeding groups typically produce a single brood per year with clutches of 2–5 eggs (Jackson 1994; Labranche & Walters 1994a). Climate change, including rising temperatures, altered precipitation regimes, and increasingly severe natural disturbances such as hurricanes, has been linked to shifts in RCW reproductive traits (Engstrom et al. 1990; Conner et al. 2005; DeMay et al. 2019; Louthan et al. 2021). Egg-laying dates have advanced in parts of the species' range (Schiegg et al. 2002), and reproductive traits such as clutch size and phenology correlate with annual weather variation (Garcia et al. 2014). These climatic sensitivities indicate clear mechanistic pathways by which weather can shape brood outcomes: (1) during laying, warm temperatures can accelerate embryonic development in early-laid eggs, intensifying size hierarchies once hatching occurs (Webb 1987; Stoleson & Beissinger 1999; Deeming 2004); (2) during brood-rearing, both heat and rainfall can alter invertebrate food availability, reduce foraging efficiency, or affect cavity microclimates, raising energetic demands and increasing the risk that smaller chicks will die (Rodríguez & Bustamante 2003; Pearce-Higgins 2010; Andreasson et al. 2020). Given these dynamics, weather during laying and brood-rearing may influence both the formation of size hierarchies and the likelihood of partial brood loss in RCWs. At the same time, cooperative breeding may buffer these risks. Helpers can increase food delivery, defend the cavity, or provide brooding and shading, thereby reducing competition within broods and helping smaller chicks survive under stressful environmental conditions (Hatchwell & Komdeur 2000; Koenig & Dickinson 2004; Russell et al. 2007).

We used multi-decade nest monitoring data from three RCW populations—Sandhills (NC), Marine Corps Base Camp Lejeune (NC), and Eglin Air Force Base (FL)—to test how weather and social factors influence late partial brood loss, focusing on within-brood size variation as a potential causal pathway. Specifically, we examined how maximum temperatures during laying, maximum temperatures and precipitation during brood rearing, and key social factors (number of males) — together with lay date as a phenological factor and clutch size as a covariate — influenced within-brood mass coefficient of variation (CoV) and subsequent brood survival outcomes. We predicted that (1) broods with greater size variation would be more likely to experience late partial brood loss, (2) higher temperatures during laying would increase chick size variation and thereby late partial brood loss, and (3) adverse brood-rearing conditions (including unusually hot or wet periods) during brood-rearing would exacerbate competition and increase late partial brood loss. This framework links environmental and social variation to their downstream consequences for brood survival, providing new insight into reproductive pressures in a threatened cooperative breeder.

Materials and Methods

We acquired banding, group composition, and reproduction data from three RCW populations: (1) an inland site in the North Carolina Sandhills (1981–2023; 813 potential breeding groups (PBGs), (2) a site on the central coast of North Carolina at Marine Corps Base Camp Lejeune (1986–2022; 136 PBGs), and (3) a Gulf Coast Florida panhandle site at Eglin Air Force Base (1995–2023; 533 PBGs; Figure 2). Monitoring of individual RCW groups was facilitated by the conspicuous resin-coated cavities excavated in living pines and by the long-term stability of territories. Each territory in the study areas was visited prior to each breeding season to determine whether it was occupied, indicated by the presence of at least one active cavity tree. Thereafter, cavities were inspected within each active territory every 7-11 days to detect and monitor reproductive attempts. At 5-10 days post hatching, nestlings were banded with a unique combination of color bands. Groups were followed post-fledging to determine the identity and sex (based on sexually dimorphic crown patches) of fledged young. Color-banded adults were identified to obtain group size and composition, and each individual was assigned a status (e.g., breeder, floater, or helper) based on behavioral observations and their age. Unbanded adults immigrating into the study areas were captured from their roost trees and color banded. Refer to Walters et al. (1988) for a more detailed description of data collection. We were only able to include years where complete data were available; thus, the site-years included in the analysis were variable based on the year data collection started for each site, with each site being analyzed separately for this analysis.

For each PBG, we included data on the number of nestlings and individual nestling mass. We assigned late partial brood loss when all banded nestlings did not fledge. We included only nests that produced at least one banded chick and at least one fledgling (Supplementary Material Table S1). The estimated clutch initiation date for each PBG was determined by using the age of the oldest nestling at banding to estimate the hatch date and subtracting 11 days (based on Ligon 1970) to determine the date the first egg was laid. Clutch initiation dates were converted to ordinal dates for consistency. To quantify within-brood size dynamics, we calculated the coefficient of variation (CoV) in chick mass, defined as the standard deviation of nestling mass within a brood divided by the mean brood mass. We examined the occurrence of late partial brood loss—defined as a binary variable indicating whether at least one chick, but not all chicks, within a brood died before fledging—and used this as the response variable in all statistical analyses. To account for non-independence, we included a unique nest identifier as a random effect in statistical models.

Weather Data and Breeding Phenology

We used weather data from 1981 to 2023 to examine how temperature and precipitation during the breeding season influenced the occurrence of partial brood loss. We obtained gridded daily maximum and total precipitation data at a 4-km spatial resolution—the finest available for the geographic and temporal extent of our study— from PRISM (PRISM Climate Group, 2023). These values are derived using a climate mapping system that combines station observations with digital elevation models and other spatial data to interpolate weather conditions across the landscape. We calculated the average daily maximum temperature (°F) and average daily precipitation (cm) during the (1) the laying period, defined as the span of egg laying prior to the onset of full incubation; and (2) the brood-rearing period, defined as the span of dates prior to chicks fledging (38-40 days old). Additionally, we created a binary variable indicating whether any days during the laying period exceeded physiological zero (>78.8 °F). Thus, the final set of weather covariates included in models were: (1) percent of laying days exceeding 78.8 °F, (2) mean maximum daily temperature during brood-rearing, and (3) mean daily precipitation during brood-rearing (Table 2).

Statistical Analysis

We evaluated the per-brood probability of late partial brood loss separately for each of the three sites. We modeled the effects of weather variables and chick size variation on the likelihood of partial brood loss. We also included other suspected predictors of late partial brood loss —- number of males in the group (i.e., breeder males and male helpers), clutch size, and lay date (Table 2; Pharr et al. 2025). We evaluated pairwise collinearity using Pearson correlation coefficients ($|r| < 0.7$). No variables were correlated, so all were retained for analysis.

We used a path analysis to evaluate hypothesized causal pathways linking weather, chick size variation, and late partial brood loss (Figure 1). Specifically, within each site we fit generalized additive models (GAMs) with random-effect smooths (bs = "re") for ClusterID (territory) and Year. First, we modeled brood-level size disparity (coefficient of variation in chick mass; CoV) as a function of weather and chick size variation using a Gaussian GAM. We then modeled the probability of late partial brood loss (0/1) as a function of CoV and the same set of predictors using a binomial (logit-link) GAM. We standardized continuous predictors (mean = 0, SD = 1) to facilitate interpretation and convergence. We reported standardized effect estimates (β) with SE and 95% CIs from the CoV model and log-odds (β), odds ratios ($OR = e^\beta$), and 95% CIs from the late-loss model. We assessed model adequacy using deviance explained (and adjusted R^2 for Gaussian fits), and residuals and dispersion were examined to verify assumptions. We conducted all analyses in R (R Core Team 2024) using the mgcv package. To visualize the hypothesized pathways, we combined effect estimates from the brood-level size disparity model and probability of late partial brood loss model into a schematic path diagram (Figure 4).

Results

We analyzed multi-decade nest monitoring data spanning 2,570 broods from the Sandhills (1981–2023), 1,546 broods from Camp Lejeune (1986–2022), and 287 broods from Eglin Air Force Base (1995–2023). Within-brood mass variation (CoV) averaged 0.26 ± 0.11 at Sandhills, 0.27 ± 0.11 at Lejeune, and 0.24 ± 0.09 at Eglin, and was moderately right-skewed, with most broods (≈ 75 %) showing CoV < 0.30. Mean chick mass clustered around 20–26 g, and typical within-brood mass ranges were small (often < 5 g) but occasionally included larger gaps (> 15–20 g).

Across sites, late partial brood loss was more frequent in broods with greater within-brood mass variation. At Sandhills, nests that experienced late brood loss had a mean chick mass CoV of 0.106 ± 0.074 ($n = 915$) compared to 0.086 ± 0.063 ($n = 1655$) for fully successful nests. At Lejeune, partial-loss nests averaged a chick mass CoV of 0.098 ± 0.083 ($n = 542$) compared to 0.082 ± 0.065 ($n = 1003$) for successful nests. At Eglin, partial-loss nests averaged a chick mass CoV of 0.102 ± 0.072 ($n = 114$) compared to 0.079 ± 0.058 ($n = 173$) for successful nests (Figure 3).

Laying-period mean daily maximum temperatures were similar for nests that did and did not experience late partial brood loss at all sites (e.g., Sandhills median 76.2 °F for nests with loss vs. 75.7 °F for nests without loss, $p = 0.529$; Eglin 81.1 °F vs. 82.1 °F, $p = 0.182$). However, the frequency of “hot days” during laying—defined as days exceeding 78.8 °F—varied strongly among sites, with a much higher fraction of broods exposed at Eglin (79.4%) than at Sandhills (31.3%) or Lejeune (36.1%). Daily maximum temperatures during the nestling period were generally higher at Eglin (mean ≈ 88.8 °F; range 84.2–95.8 °F) than Sandhills (83.9 °F; 71.2–91.3 °F) or Lejeune (83.4 °F; 75.1–91.8 °F).

Gaussian GAMs showed that the odds of late partial brood loss increased with higher chick mass CoV, with weather and social factors shaping chick mass CoV or exerting additional direct effects on late partial brood loss. At Sandhills, later lay dates ($\beta = 0.001$, $SE = 0.0002$, $p < 0.001$), larger clutches ($\beta = 0.006$, $SE = 0.003$, $p = 0.047$), and lower mean brood-rearing precipitation ($\beta = -0.087$, $SE = 0.039$, $p = 0.027$) increased chick mass CoV, which in turn sharply increased the odds of late partial brood loss (OR = 6.60, 95 % CI [2.74, 15.88]);

precipitation also had a strong direct positive effect on brood loss (OR = 149.73, 95 % CI [5.81, 3862.28]), whereas larger clutch sizes increased risk (OR = 1.28, 95 % CI [1.10, 1.48]) and more males reduced it (OR = 0.73, 95 % CI [0.64, 0.82]). At Lejeune, warmer brood-rearing mean daily maximum temperatures (β = 0.094, SE = 0.042, p = 0.024) and larger clutches (β = 0.014, SE = 0.005, p = 0.003) increased chick mass CoV, which in turn elevated late partial brood loss (OR = 5.94, 95 % CI [2.43, 14.50]); clutch size also exerted an additional direct positive effect on the risk of late partial brood loss (OR = 1.41, 95 % CI [1.11, 1.79]). At Eglin, higher brood-rearing precipitation increased chick mass CoV (β = 0.163, SE = 0.080, p = 0.043), and higher chick mass CoV subsequently increased the odds of late loss (OR = 1.44, 95 % CI [1.10, 1.88]).

Discussion

In all three populations, high within-brood mass variation (chick mass CoV) was the strongest predictor of late partial brood loss. Broods with greater size hierarchies consistently lost chicks, providing support for the brood-reduction hypothesis (Lack 1968; Mock & Parker 1997), which posits that asynchronous hatching produces competitive asymmetries that can reduce brood size to match food availability. Other adaptive hypotheses for hatching asynchrony—such as the nest-failure (Hussell 1972; Clark & Wilson 1981), egg-viability (Arnold et al. 1987), and peak load reduction hypotheses (Mock & Schwagmeyer 1990; Siegel et al. 1999)—focus more on the initiation of incubation than on its consequences, yet all converge on the expectation that environmental conditions will shape brood survival through their effects on chick size hierarchies.

Site-specific differences in the drivers of chick mass variation suggest that multiple causal pathways can generate size hierarchies in RCWs. At Sandhills, later nesting, larger clutches, and reduced precipitation increased chick mass CoV, indicating that extended laying periods and limited rainfall exacerbate size hierarchies. At Lejeune, higher mean daily maximum temperatures during brood rearing and larger clutches increased chick mass CoV, consistent with the egg-viability hypothesis in that high laying-period temperatures may accelerate early embryo development, creating greater asymmetries among chicks. At Eglin, greater precipitation during brood rearing increased chick mass CoV, likely because heavy rainfall reduces foraging efficiency by limiting insect activity and increases nest microclimate stress through chilling or damp conditions. This site-specific effect, together with the temperature-driven asymmetries observed at Lejeune and the clutch size/phenology effects at Sandhills, shows that weather shapes competitive hierarchies through multiple pathways—including altered prey availability, reduced provisioning rates, and adverse nest microclimates—and is broadly consistent with the sibling-competition hypothesis (Forbes & Glassey 2000; Magrath 1990), which emphasizes the role of environmental stressors in amplifying competitive disadvantages of smaller nestlings.

Heavy precipitation can bypass adaptive mechanisms of hatching asynchrony and directly drive mortality through proximate stressors such as reduced provisioning, chilling of nestlings, or disrupted foraging (Rodríguez & Bustamante 2003; Pearce-Higgins 2010; Andreasson et al. 2020). In the Sandhills, this dynamic was evident: heavy rainfall directly elevated the probability of late partial brood loss, even as it slightly reduced chick mass CoV. By contrast, at Lejeune and Eglin, weather effects on brood survival were only indirect, operating through increased within-brood size variation rather than through direct mortality pathways.

Clutch size further influenced brood outcomes, with larger clutches associated with greater chick mass CoV and greater risk of partial brood loss at Sandhills and Lejeune. This result is consistent with the brood-reduction hypothesis’s framing of overproduction as reproductive “insurance” in unpredictable environments (Lack 1947; O’Connor 1984), as well as with life-history theory predicting trade-offs between offspring number and quality (Trivers 1972). In cooperative breeders, these trade-offs may be partially offset by the presence of helpers.

Indeed, across sites, more male helpers reduced the likelihood of late partial brood loss, highlighting the buffering role of cooperative breeding (Emlen 1997; Mumme 1997; Khan & Walters 2002). This effect was strongest at Sandhills, where helpers likely mitigated the consequences of both environmental stress and large clutch sizes. At the other sites, helper effects were weaker, which may reflect genuine biological differences in helper behavior, ecological context, or reduced statistical power due to smaller sample sizes. Taken together, these findings emphasize that social buffering can offset some of the risks imposed by environmental variability, but it is not absolute and may be overwhelmed under stressful seasonal or site-specific conditions.

Our results indicate that weather rarely drives late partial brood loss directly; instead, weather acts mainly by amplifying size variation among chicks, which increases the likelihood that smaller nestlings will die. This positions within-brood mass variation (i.e., chick mass CoV) as a potential early-warning indicator of weather-related reproductive risk. As climate variability intensifies, tracking chick mass variation alongside environmental conditions could help managers anticipate reproductive shortfalls before they occur. Our findings also show that male helpers can buffer some of the costs of hot or wet post-hatch conditions and later-season breeding—likely by stabilizing provisioning and nest care—though this buffering is incomplete and can be overwhelmed in certain contexts (e.g., wet post-hatch periods or late laying at Sandhills). Future work should aim to clarify the behavioral mechanisms by which helpers reduce brood loss (e.g., more consistent provisioning, brooding/shading, cavity maintenance) and to integrate behavioral, microclimate, and growth monitoring. Such site-specific monitoring could help predict where cooperative breeding will continue to stabilize reproduction and where climate stress may outstrip group buffering, leading to reduced productivity.

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Table 4.1. Major hypotheses proposed to explain the evolution of hatching asynchrony in birds, including the core idea of each hypothesis, its predicted adaptive benefit, and key references.

Hypothesis	**Core Idea**	**Predicted Benefit**	**Testable Predictions (linked to variables)**	**Key References**
Brood-reduction hypothesis	Parents begin incubation before the clutch is complete, producing size hierarchies among chicks. If food becomes limited, smaller, later-hatched chicks die, reducing brood size to match food availability.	Mechanism to hedge against unpredictable resources; ensures at least some offspring survive.	Broods with greater within-brood mass variation (CoV) are more likely to experience late brood loss. Larger clutches increase the likelihood of partial brood loss, reflecting overproduction as reproductive insurance.	Lack 1968; Mock & Parker 1997
Nest-failure (insurance) hypothesis	Early incubation accelerates hatching so that chicks fledge earlier, reducing total time the nest is exposed to predation or other risks.	Shorter nesting period lowers risk of complete nest failure.	Later laying dates extend the nesting season and increase brood loss risk, potentially mediated by CoV if late nests experience greater environmental stress.	Hussell 1972; Clark & Wilson 1981

Egg-viability hypothesis	Incubation begins early to prevent early-laid eggs from cooling/drying out or losing viability during extended pre-incubation periods.	Maximizes hatchability across the clutch.	High temperatures during laying accelerate early embryo development, increasing mass variation among chicks and the likelihood of brood reduction.	Arnold et al. 1987
Peak load reduction hypothesis	Spreading hatching distributes parental feeding effort across time rather than concentrating it in a single peak demand period.	Reduces the likelihood of an unsustainable provisioning peak, allowing parents to maintain consistent care.	Larger clutches increase within-brood mass variation (CoV), distributing peak feeding effort across nestlings. If provisioning is limited, brood loss risk rises. The presence of male helpers should reduce loss risk by buffering provisioning demands and stabilizing care.	Siegel et al. 1999; Mock & Schwagmeyer 1990

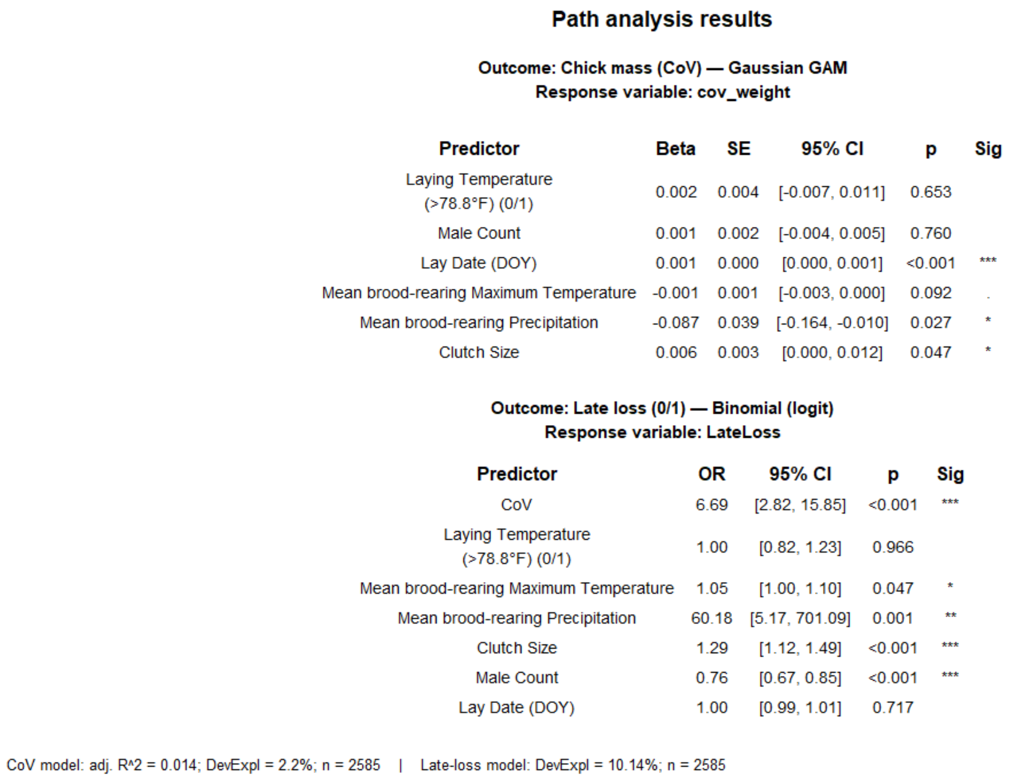
Sibling-competition (signals) hypothesis	Size hierarchies allow parents to allocate food more efficiently by focusing on competitive, vigorous chicks.	Increases efficiency of parental investment.	Environmental stress, including high temperatures or high/low precipitation during brood rearing, increases mass variation and brood reduction. Helper presence buffers smaller chicks against these competitive disadvantages.	Forbes & Glassey 2000; Magrath 1990

Table 4.2. Independent and dependent variables used in the development climatic influence on the outcome of late partial brood loss models for each site. Variables are annotated as follows: (†) denotes a fixed and random variable and (§) denotes a random effect only.

Variable	Variable description
Year †	Year
Cluster ID §	Combined Cluster ID and Year
Lay Date	Estimated clutch initiation day
Clutch Size	Number of eggs
Male Count	Sum of breeder male and male helpers per cluster
CoV Chick Mass	Coefficient of variation (SD ÷ mean) of chick mass within each brood at standardized banding age within each brood, each year.
Laying Days above 78.8	Indicates if mean max daily temperature during laying exceeded 78.8 °F (1 = yes, 0 = no). Spatial resolution: 4 km; represents conditions before full incubation.
Mean Brood-rearing Maximum Temperature	Average Maximum Temperature (°F) of pre-fledging days. Spatial resolution: 4 km.

Mean Brood-rearing Precipitation	Average precipitation (inches) of pre-fledging days. Spatial resolution: 4 km.

Table 4.3. Path diagram results for Sandhills. Later lay dates, larger clutches, and lower brood-rearing precipitation were associated with greater within-brood mass disparity (CoV). In turn, higher CoV strongly increased the likelihood of late partial brood loss (OR ≈ 6.7). Clutch size also had a direct positive effect on late loss, while higher male numbers reduced risk. Precipitation showed contrasting effects—decreasing mass disparity but directly increasing late loss—highlighting its complex and stage-specific roles.



Path analysis results

Outcome: Chick mass (CoV) — Gaussian GAM
Response variable: cov_weight

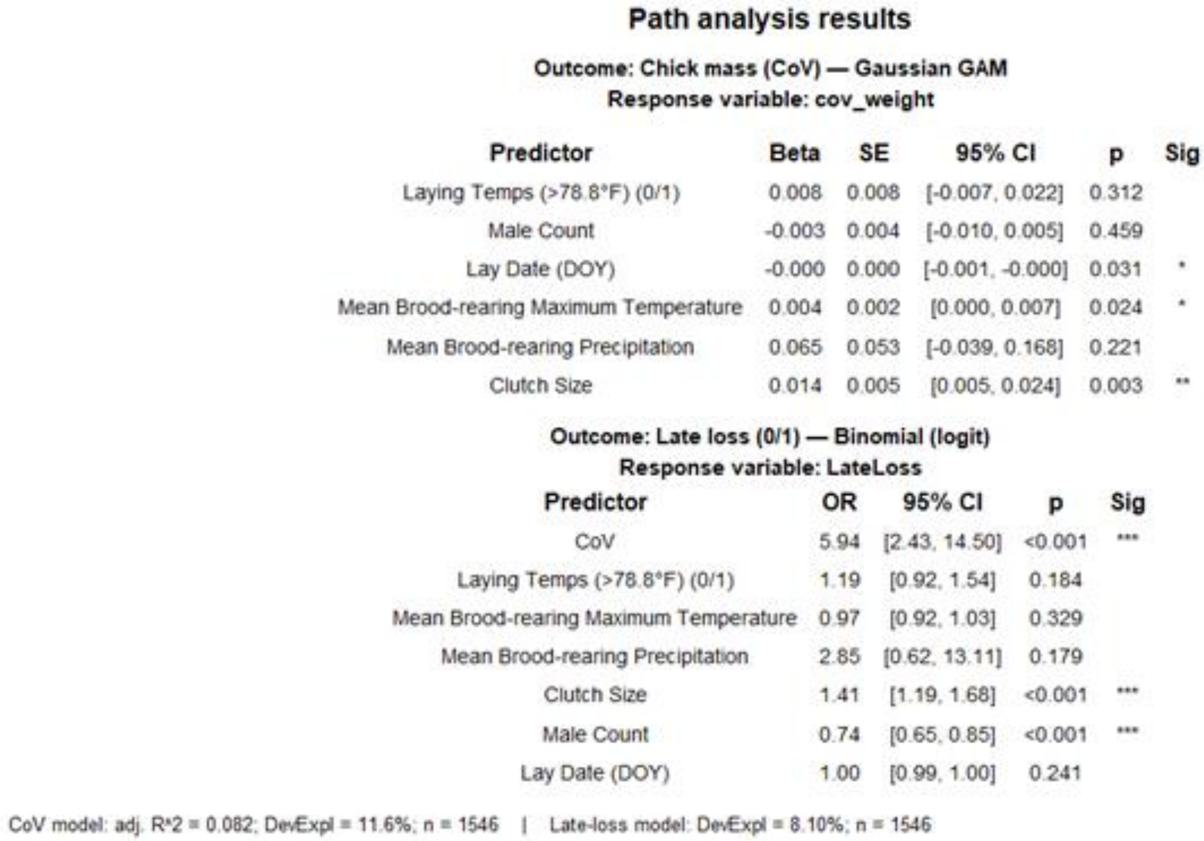
Predictor	Beta	SE	95% CI	p	Sig
Laying Temperature (>78.8°F) (0/1)	0.002	0.004	[-0.007, 0.011]	0.653	
Male Count	0.001	0.002	[-0.004, 0.005]	0.760	
Lay Date (DOY)	0.001	0.000	[0.000, 0.001]	<0.001	***
Mean brood-rearing Maximum Temperature	-0.001	0.001	[-0.003, 0.000]	0.092	.
Mean brood-rearing Precipitation	-0.087	0.039	[-0.164, -0.010]	0.027	*
Clutch Size	0.006	0.003	[0.000, 0.012]	0.047	*

Outcome: Late loss (0/1) — Binomial (logit)
Response variable: LateLoss

Predictor	OR	95% CI	p	Sig
CoV	6.69	[2.82, 15.85]	<0.001	***
Laying Temperature (>78.8°F) (0/1)	1.00	[0.82, 1.23]	0.966	
Mean brood-rearing Maximum Temperature	1.05	[1.00, 1.10]	0.047	*
Mean brood-rearing Precipitation	60.18	[5.17, 701.09]	0.001	**
Clutch Size	1.29	[1.12, 1.49]	<0.001	***
Male Count	0.76	[0.67, 0.85]	<0.001	***
Lay Date (DOY)	1.00	[0.99, 1.01]	0.717	

CoV model: adj. R^2 = 0.014; DevExpl = 2.2%; n = 2585 | Late-loss model: DevExpl = 10.14%; n = 2585

Table 4.4. Path diagram results for Lejeune. Larger clutches and warmer mean brood-rearing temperatures were associated with greater within-brood mass disparity (CoV). In turn, higher CoV strongly increased the likelihood of late partial brood loss (nearly sixfold per SD increase). Clutch size also had a direct positive effect on late loss, whereas direct effects of temperature, precipitation, lay date, and male count were weak and non-significant.



Path analysis results

Outcome: Chick mass (CoV) — Gaussian GAM
Response variable: cov_weight

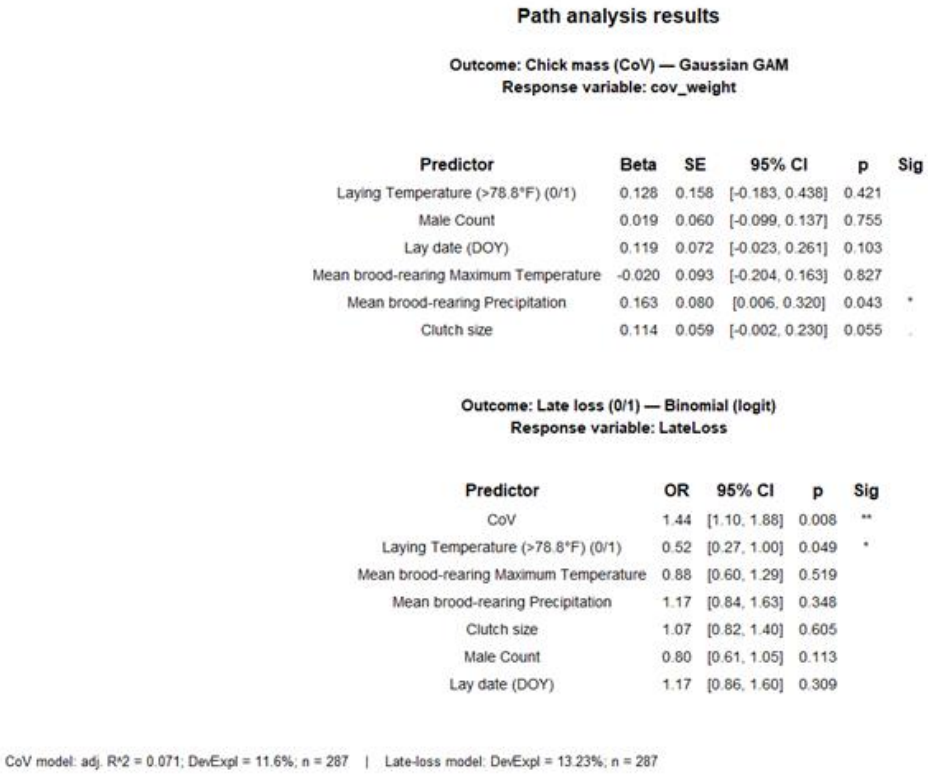
Predictor	Beta	SE	95% CI	p	Sig
Laying Temps (>78.8°F) (0/1)	0.008	0.008	[-0.007, 0.022]	0.312	
Male Count	-0.003	0.004	[-0.010, 0.005]	0.459	
Lay Date (DOY)	-0.000	0.000	[-0.001, -0.000]	0.031	*
Mean Brood-rearing Maximum Temperature	0.004	0.002	[0.000, 0.007]	0.024	*
Mean Brood-rearing Precipitation	0.065	0.053	[-0.039, 0.168]	0.221	
Clutch Size	0.014	0.005	[0.005, 0.024]	0.003	**

Outcome: Late loss (0/1) — Binomial (logit)
Response variable: LateLoss

Predictor	OR	95% CI	p	Sig
CoV	5.94	[2.43, 14.50]	<0.001	***
Laying Temps (>78.8°F) (0/1)	1.19	[0.92, 1.54]	0.184	
Mean Brood-rearing Maximum Temperature	0.97	[0.92, 1.03]	0.329	
Mean Brood-rearing Precipitation	2.85	[0.62, 13.11]	0.179	
Clutch Size	1.41	[1.19, 1.68]	<0.001	***
Male Count	0.74	[0.65, 0.85]	<0.001	***
Lay Date (DOY)	1.00	[0.99, 1.00]	0.241	

CoV model: adj. R^2 = 0.082; DevExpl = 11.6%; n = 1546 | Late-loss model: DevExpl = 8.10%; n = 1546

Table 4.5. Path diagram results for Eglin. Higher brood-rearing precipitation was significantly associated with greater within-brood mass disparity (CoV), while clutch size showed a weaker, marginally positive association. In turn, higher CoV increased the likelihood of late partial brood loss (~44% per SD increase). Exposure to laying temperatures above 78.8 °F was associated with a lower probability of late loss. Other predictors showed weak and non-significant effects.



Path analysis results

Outcome: Chick mass (CoV) — Gaussian GAM
Response variable: cov_weight

Predictor	Beta	SE	95% CI	p	Sig
Laying Temperature (>78.8°F) (0/1)	0.128	0.158	[-0.183, 0.438]	0.421	
Male Count	0.019	0.060	[-0.099, 0.137]	0.755	
Lay date (DOY)	0.119	0.072	[-0.023, 0.261]	0.103	
Mean brood-rearing Maximum Temperature	-0.020	0.093	[-0.204, 0.163]	0.827	
Mean brood-rearing Precipitation	0.163	0.080	[0.006, 0.320]	0.043	*
Clutch size	0.114	0.059	[-0.002, 0.230]	0.055	.

Outcome: Late loss (0/1) — Binomial (logit)
Response variable: LateLoss

Predictor	OR	95% CI	p	Sig
CoV	1.44	[1.10, 1.88]	0.008	**
Laying Temperature (>78.8°F) (0/1)	0.52	[0.27, 1.00]	0.049	*
Mean brood-rearing Maximum Temperature	0.88	[0.60, 1.29]	0.519	
Mean brood-rearing Precipitation	1.17	[0.84, 1.63]	0.348	
Clutch size	1.07	[0.82, 1.40]	0.605	
Male Count	0.80	[0.61, 1.05]	0.113	
Lay date (DOY)	1.17	[0.86, 1.60]	0.309	

CoV model: adj. R^2 = 0.071; DevExpl = 11.6%; n = 287 | Late-loss model: DevExpl = 13.23%; n = 287

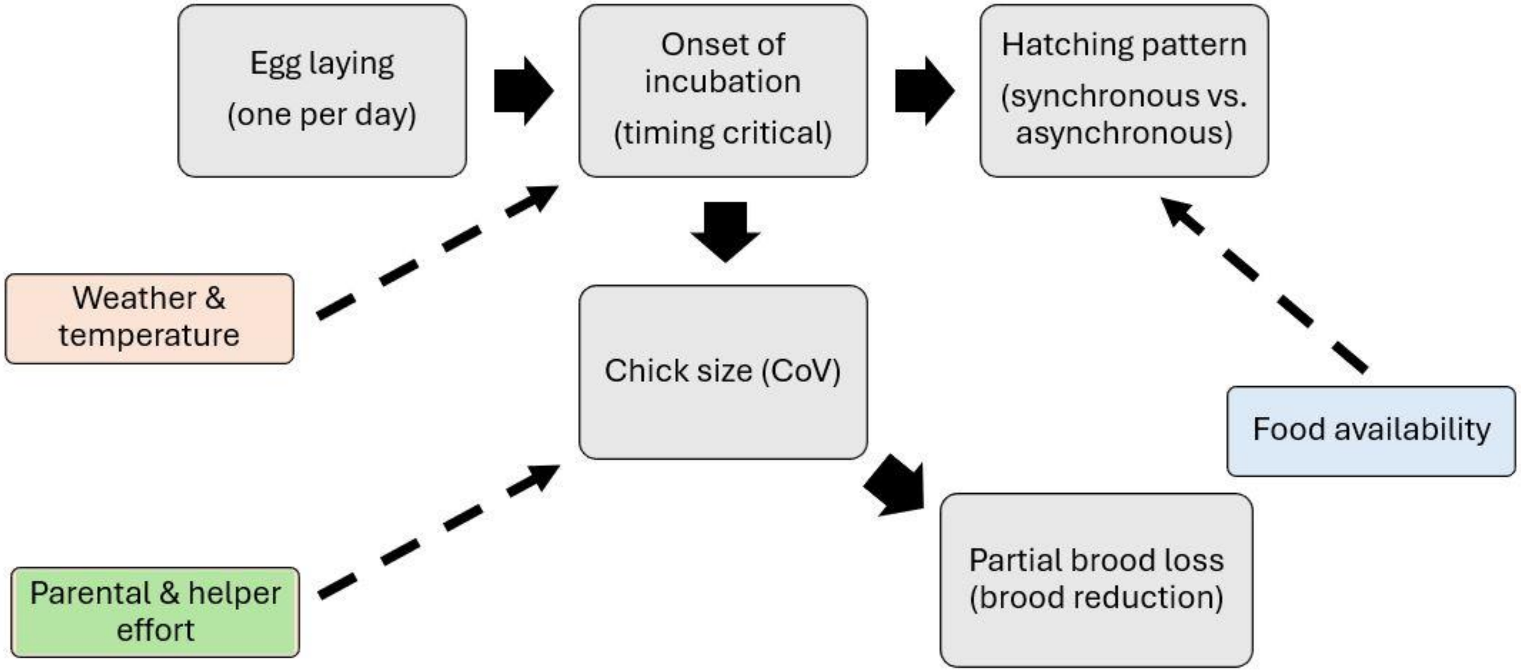


Figure 4.1. Conceptual diagram linking the timing of laying and incubation onset to hatching patterns, chick size hierarchies, and partial brood loss. Weather and temperature can influence the timing of incubation and hatching, food availability can affect chick growth and survival, and parental or helper effort mediates chick outcomes. Together, these factors determine whether asynchronous hatching leads to brood reduction.

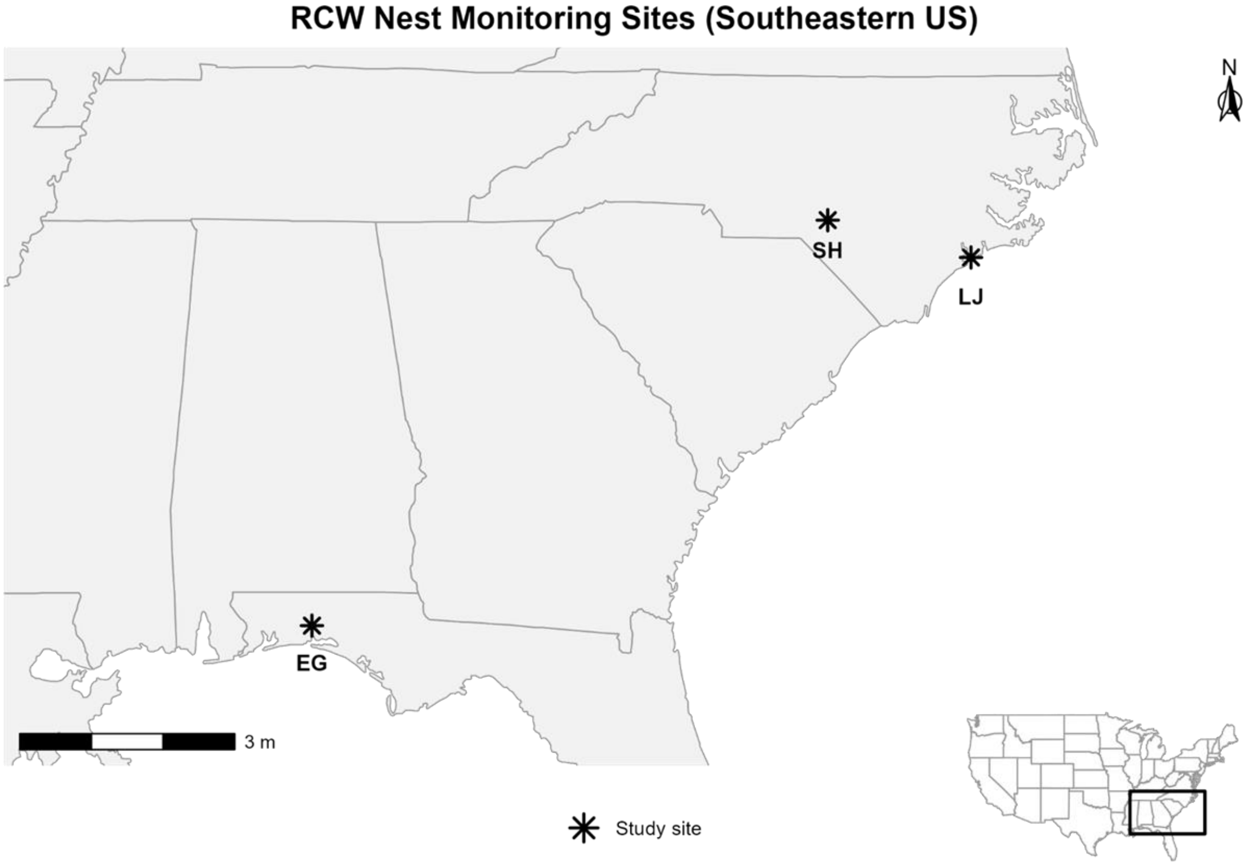


Figure 4.2. Location of the Sandhills, Lejeune, and Eglin sites where we monitored Red-cockaded Woodpecker (*Dryobates borealis*) reproduction from 1981 to 2023 in the southeastern U.S.

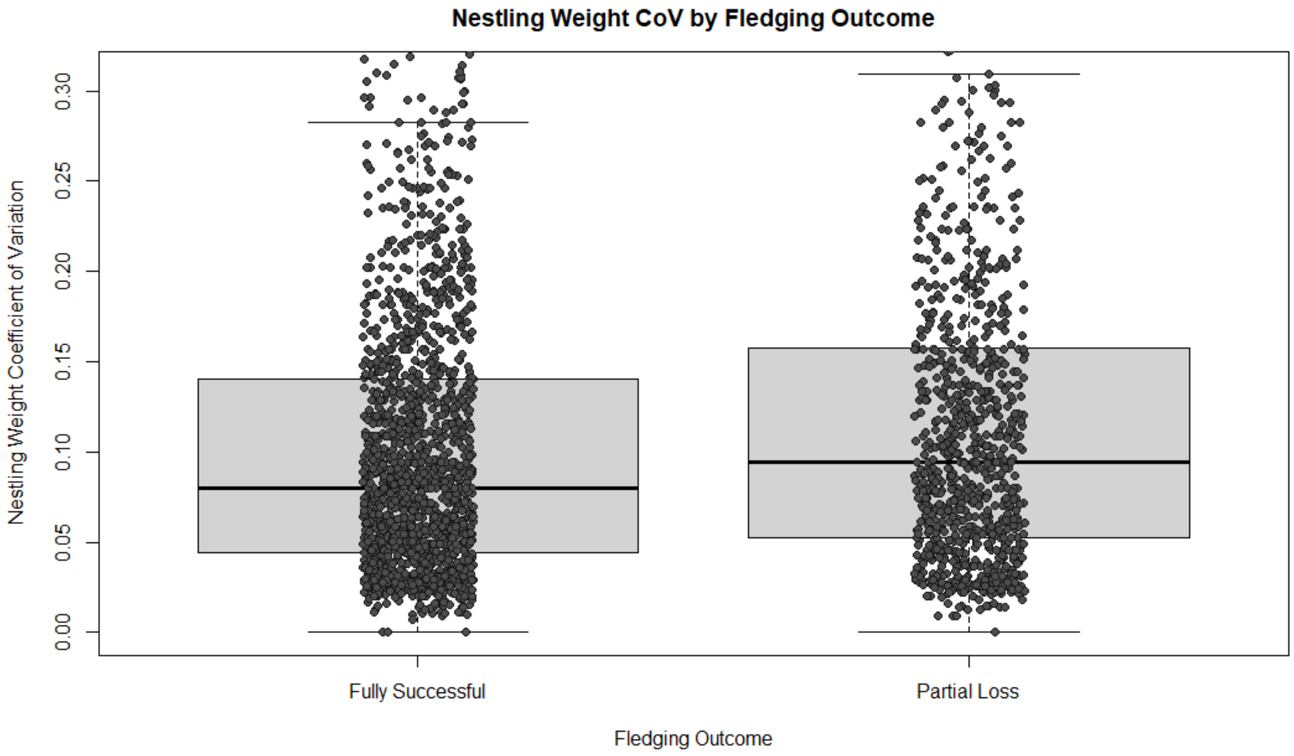


Figure 4.3. Nestling mass disparity (CoV) by fledgling outcome. Boxplots (line = median, box = IQR, whiskers = 1.5×IQR, points = outliers) compare within-brood CoV of nestling mass at the standardized banding age for broods that were fully successful vs. those with partial brood loss (late loss) for Sandhills. Where shown, brackets indicate Wilcoxon rank-sum tests; higher CoV in the partial-loss group reflects greater within-brood inequality prior to fledging. Nestling mass disparity (CoV) by fledgling outcome (fully successful vs. late loss) at each site. Late-loss broods show higher CoV (Wilcoxon $p = 9.6\times10^{-6}$).

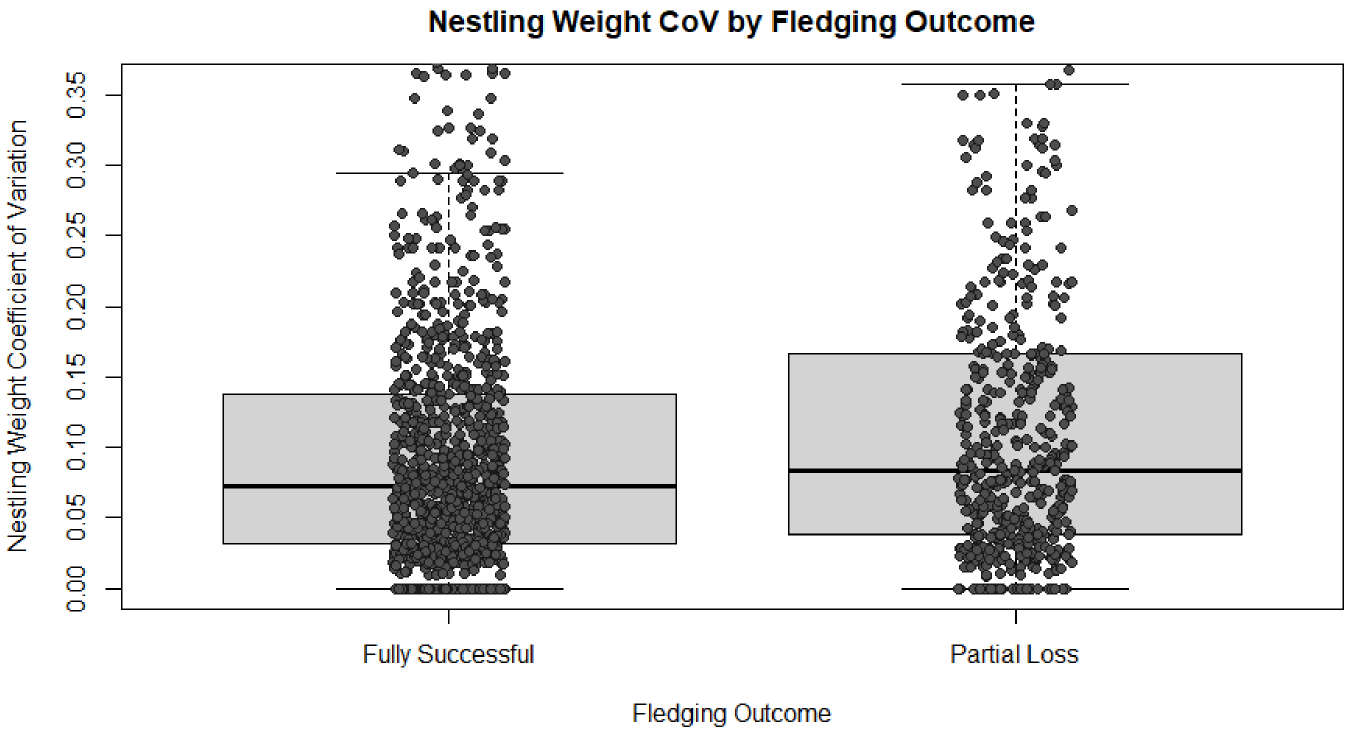


Figure 4.4. Nestling mass disparity (CoV) by fledgling outcome. Boxplots (line = median, box = IQR, whiskers = 1.5×IQR, points = outliers) compare within-brood CoV of nestling mass at the standardized banding age for broods that were fully successful vs. those with partial brood loss (late loss) for Lejeune. Where shown, brackets indicate Wilcoxon rank-sum tests; higher CoV in the partial-loss group reflects greater within-brood inequality prior to fledging. Nestling mass disparity (CoV) by fledgling outcome (fully successful vs. late loss) at each site. Late-loss broods show higher CoV (Wilcoxon *p* = 0.002).

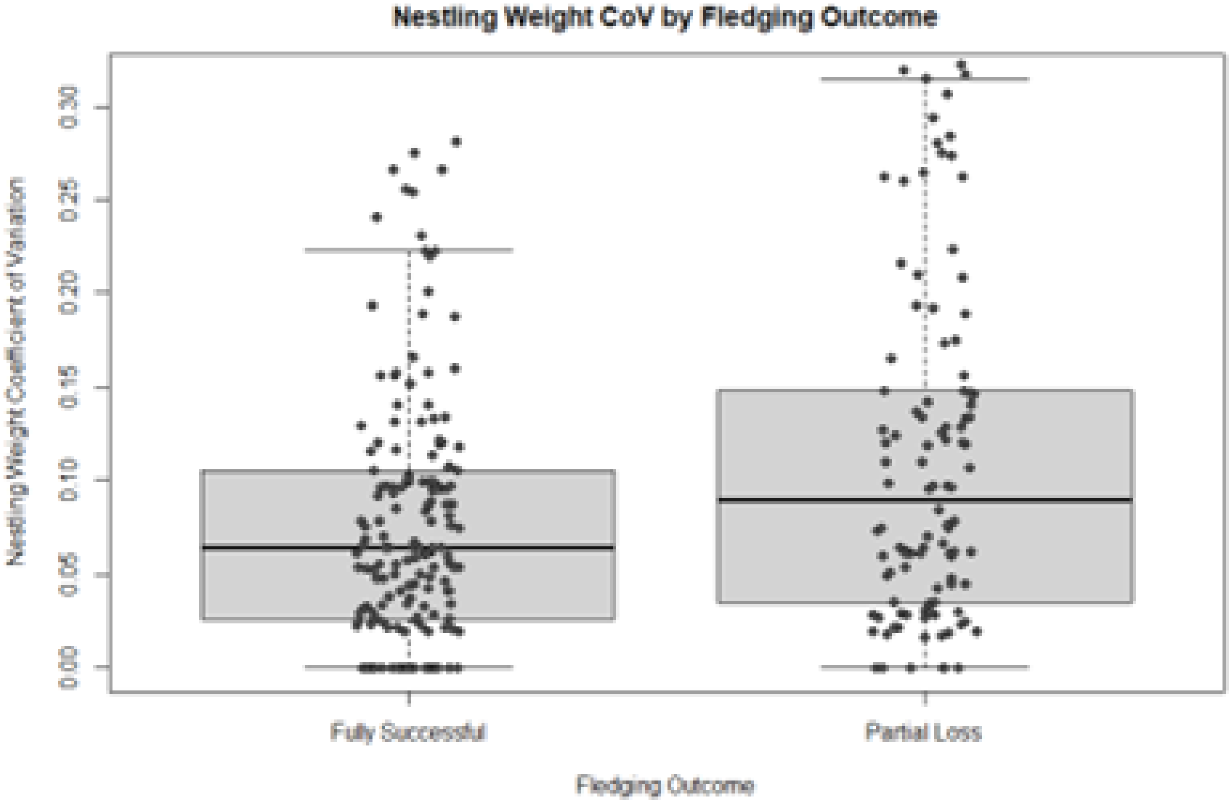


Figure 4.5. Nestling mass disparity (CoV) by fledgling outcome. Boxplots (line = median, box = IQR, whiskers = 1.5×IQR, points = outliers) compare within-brood CoV of nestling mass at the standardized banding age for broods that were fully successful vs. those with partial brood loss (late loss) for Eglin. Where shown, brackets indicate Wilcoxon rank-sum tests; higher CoV in the partial-loss group reflects greater within-brood inequality prior to fledging. Nestling mass disparity (CoV) by fledgling outcome (fully successful vs. late loss) at each site. Late-loss broods show higher CoV (Wilcoxon $p = 0.0026$).

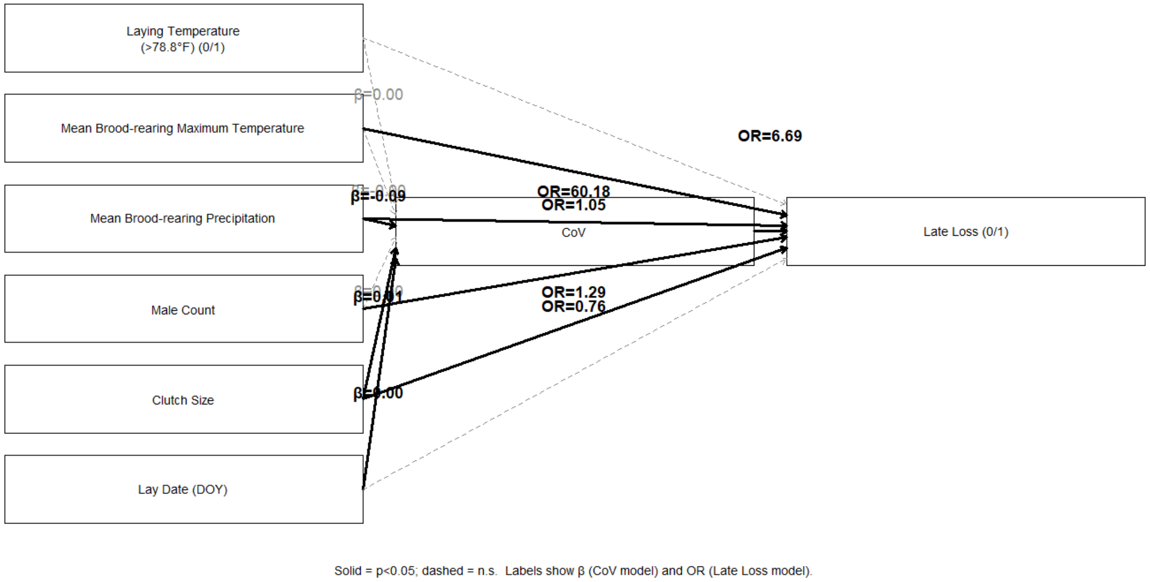
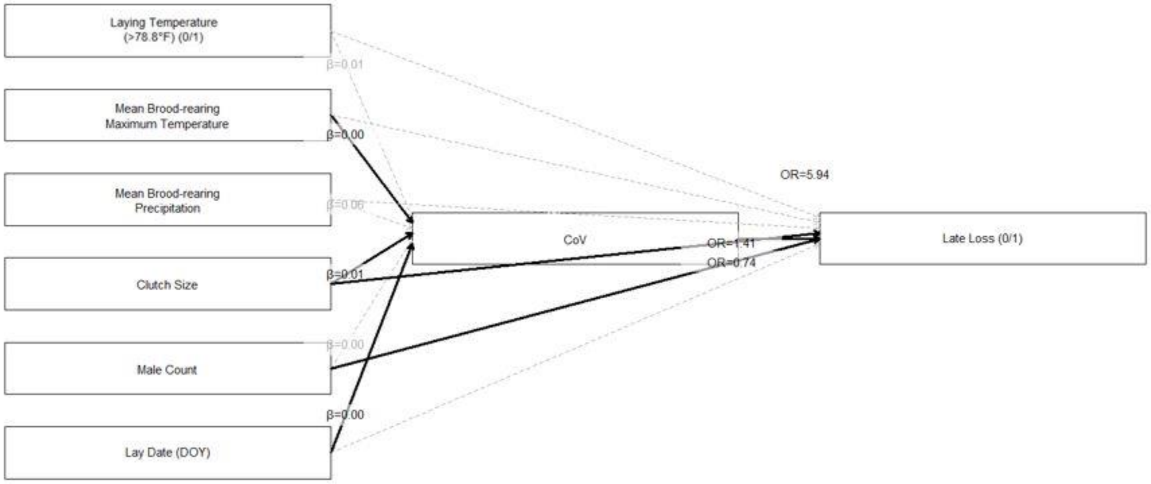


Figure 4.6. Path diagrams for Sandhills showing links from brood-rearing climate and social covariates (left) to Disparity (CoV) (middle) and Late loss (0/1) (right). Arrows into CoV are labeled with standardized β from Gaussian GAMs; arrows into Late loss show ORs from binomial GAMs; solid = $p < 0.05$, dashed = n.s. All continuous predictors were z-scored; random-effect smooths for ClusterID and Year were included but are not drawn. Later lay dates, larger clutches, and lower precipitation increased CoV, which strongly elevated late-loss risk (OR ≈ 6.7); clutch size also directly increased risk (OR ≈ 1.3), more males reduced it (OR ≈ 0.7), and precipitation showed opposing indirect (negative) and direct (positive; OR ≈ 60) effects.



Solid = p<0.05; dashed = n.s. Labels show β (CoV model) and OR (Late Loss model).

Figure 4.7. Path diagrams for Lejuene showing links from brood-rearing climate and social covariates (left) to Disparity (CoV) (middle) and Late loss (0/1) (right). Arrows into CoV are labeled with standardized β from Gaussian GAMs; arrows into Late loss show ORs from binomial GAMs; solid = $p < 0.05$, dashed = n.s. All continuous predictors were z-scored; random-effect smooths for ClusterID and Year were included but are not drawn. Warmer brood-rearing temperatures and larger clutches increased CoV, which increased late-loss risk (OR ≈ 5.9), with an additional direct effect of clutch size.

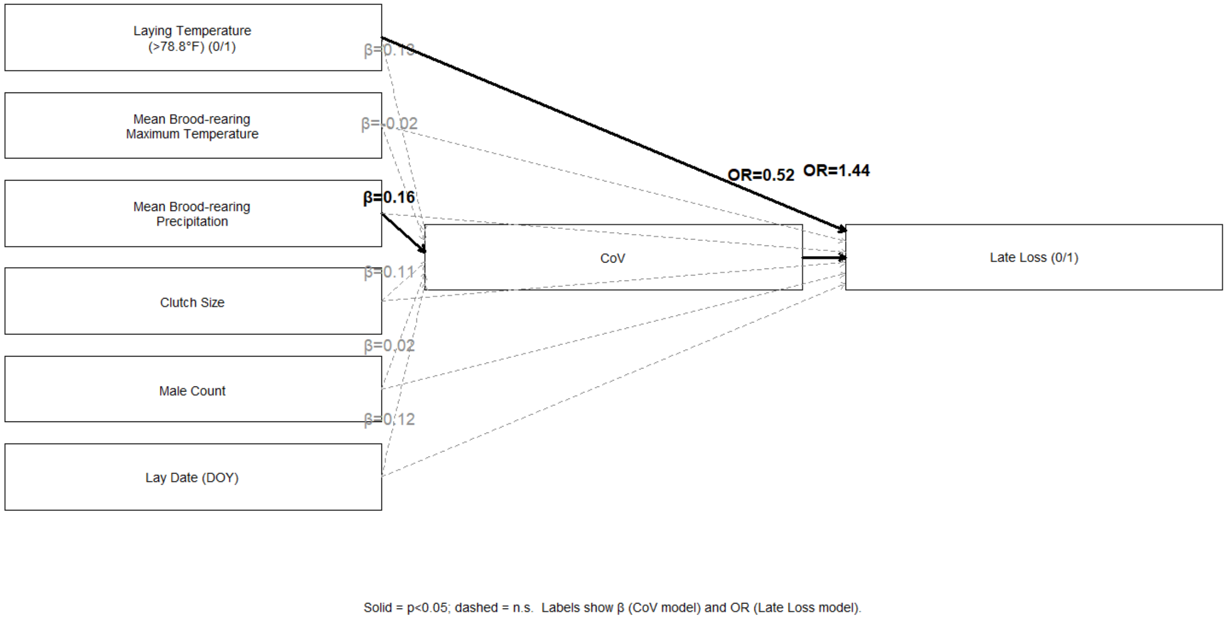


Figure 4.8. Path diagrams for Lejuene showing links from brood-rearing climate and social covariates (left) to Disparity (CoV) (middle) and Late loss (0/1) (right). Arrows into CoV are labeled with standardized β from Gaussian GAMs; arrows into Late loss show ORs from binomial GAMs; solid = $p < 0.05$, dashed = n.s. All continuous predictors were z-scored; random-effect smooths for ClusterID and Year were included but are not drawn. Eglin—precipitation increased CoV, which increased late-loss risk (OR ≈ 1.4); other direct paths were weak.

CHAPTER 6: CONCLUSION

This dissertation investigated the ecological and social drivers of partial brood loss in the Red-cockaded Woodpecker (*Dryobates borealis*), a federally threatened cooperative breeder (USFWS 2020; Walters et al. 1988, 1990). By leveraging multi-decade nest monitoring datasets across three southeastern populations, I examined how density, weather, and within-brood dynamics shape reproductive outcomes in this species.

In Chapter One, I tested whether increasing population density contributed to rising rates of brood loss. Across all three populations, I found no support for density-dependent effects on either early or late brood loss, despite concurrent increases in both density and brood loss over time. These results suggest that reproductive decline is not being driven by population recovery and highlight the need to focus on density-independent mechanisms (Both 1998; Dhondt et al. 1992; Walters 1991).

In Chapter Two, I evaluated how weather influences reproductive timing and early brood loss. Temperature and rainfall effects were largely site-specific: while warmer post-hatch temperatures increased hatching probability in the Sandhills population, no consistent weather effects were detected in the other two populations. Clutch initiation showed little evidence of phenological adjustment to rising temperatures, suggesting that RCWs may remain exposed to climate-driven challenges (Visser et al. 2004; DeMay & Walters 2019; Parmesan & Yohe 2003).

In Chapter Three, I explored the role of within-brood size hierarchies as a mechanism of late brood loss. Higher chick mass Coefficient of Variation (CoV) was consistently associated with greater late brood loss across sites, revealing brood size inequality as the strongest and most consistent predictor of reproductive failure (O’Connor 1984; Magrath 1990; Mock & Parker

1997). Weather influenced brood outcomes primarily indirectly—by shaping chick size variation. Site-specific patterns showed that temperature, precipitation, clutch size, and timing of laying each contributed to variation in brood size hierarchies and subsequent brood loss.

Together, these chapters demonstrate that partial brood loss in RCWs is shaped less by density-dependent pressures than by interactions among weather, timing, clutch structure, and chick size variation. This work reveals that brood reduction in cooperative breeders arises from complex pathways linking environmental conditions, developmental dynamics, and social context (Cockburn 1998; Koenig & Dickinson 2016; Rubenstein & Lovette 2007). By clarifying the mechanisms behind reproductive pressures, this dissertation provides new insight into the vulnerabilities and resilience of cooperative breeders under ongoing climate change—and offers a foundation for conservation strategies that account for both ecological variability and social structure in this threatened species.

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APPENDICES

Table B.1. Summary statistics for the occurrence of early partial brood loss (EPBL) for Sandhills, Lejeune, and Eglin.

	Sandhills						*Lejeune*						*Eglin*					
	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max
Continuous																		
Year *(and categorical)*	1980	2000	2012	2008	2018	2023	1986	2001	2009	2008	2017	2022	1995	2005	2012	2010	2017	2023
Clutch Size	2	3	4	3	4	5	2	3	4	3	4	5	2	3	3	3	4	5
Male Count	0	1	2	1	2	5	0	1	2	1	2	6	0	1	2	1	2	5
Female Count	0	1	1	1	1	3	1	1	1	1	1	4	1	1	1	1	1	3
Total Adults	1	2	3	2	3	7	1	2	3	3	4	8	1	2	3	2	3	6
Adults per Hectare	0.00	0.01	0.02	0.02	0.03	0.12	0.00	0.02	0.03	0.03	0.04	0.11	0.00	0.02	0.03	0.04	0.04	0.23
Group Density (ha)	27.90	103.85	138.12	138.24	180.77	200.97	37.04	74.92	92.06	98.93	117.78	192.33	25.70	59.08	83.47	88.80	117.18	200.97
Floater Count	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	2
Lay Date	101	116	121	122	127	164	99	119	124	124	130	170	87	112	118	119	125	170
Categorical																		
Total Clusters(n)	n = 2274						n = 1502						n = 513					

Table B.2. Summary statistics for the occurrence of late partial brood loss (LPBL) for Sandhills, Lejeune, and Eglin.

	Sandhills						*Lejeune*						*Eglin*					
	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max
Continuous																		
Year (and categorical)	1980	2001	2011	2008	2018	2023	1986	2001	2009	2008	2016	2022	1995	2004	2012	2010	2017	2023
Clutch Size	2	3	4	3	4	5	2	3	4	3	4	5	2	3	3	3.22	4	5
Male Count	0	1	2	1	2	5	0	1	2	1	2	6	0	1	2	1	2	5
Female Count	0	1	1	1	1	3	1	1	1	1	1	4	1	1	1	1	1	3
Total Adults	1	2	3	2	3	7	2	2	3	3	4	8	2	2	3	2	4	6
Adults per Hectare	0.00	0.01	0.02	0.02	0.03	0.12	0.00	0.02	0.03	0.03	0.04	0.11	0.00	0.02	0.03	0.04	0.04	0.23
Group Density (ha)	27.90	115.03	147.01	145.63	184.84	200.97	37.04	74.92	92.05	99.14	117.78	200.97	25.70	59.08	83.47	88.24	108.76	200.97
Floater Count	0	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	1
Lay Date	101	115	121	121	126	161	99	119	123	124	129	156	87	112	118	117	123	170
Categorical																		
Total Clusters (n)	n = 1903						n = 1238						n = 370					

Table B.3. Variance Inflation Factor (VIF) summary among variables for the occurrence of early and late partial brood loss (EPBL and LPBL) for Sandhills, Lejeune, and Eglin. The *Total Adults* variable was excluded from the VIF summary and our global model due to perfect collinearity with its component variables, *Male Count* and *Female Count*.

	Sandhills		*Lejeune*		*Eglin*	
	EPBL	LPBL	EPBL	LPBL	EPBL	LPBL
Term						
Year	1.15	1.15	1.08	1.09	1.32	1.47
Clutch Size	1.11	1.09	1.10	1.08	1.08	1.08
Male Count	2.47	2.77	4.60	4.73	1.94	2.00
Female Count	1.20	1.26	2.00	2.08	1.14	1.14
Adults per Hectare	5.73	6.34	9.92	10.29	3.53	3.63
Group Density (ha)	3.61	3.77	4.55	4.66	2.59	2.68
Floater Count	1.01	1.01	1.01	1.01	1.03	1.05
Lay Date	1.14	1.12	1.10	1.10	1.27	1.38
Total Clusters (n)	**n = 2274**	**n = 1903**	**n = 1502**	**n = 1238**	**n = 513**	**n = 370**

Table B.4. Model summaries for the occurrence of early and late partial brood loss (EPBL and LPBL) across Sandhills, Lejeune, and Eglin. Models were ranked by AICc, and those with ΔAICc ≤ 2 are presented.

	Model Description	K (df)	-2LogLik	AIC_c	ΔAIC_c	w
Site: Sandhills **Brood Loss Type: EPBL**						
	Male Count + Female Count + Clutch Size + Year + Group Density + Lay Date + Male Count * Clutch Size + Male Count*Year + (Cluster) + (Year)	11	-1238.84	2499.80	0.00	0.22
	Clutch Size + Male Count + Female Count + Year + Lay Date + Male Count * Clutch Size + Male Count*Year + (Cluster) + (Year)	10	-1239.94	2499.99	0.18	0.20
	Male Count + Female Count + Clutch Size + Floater Count + Year + Lay Date + Male Count *	11	-1239.15	2500.42	0.61	0.16

	Clutch Size + Male Count * Year + (Cluster) + (Year)					
	Group Density + Male Count + Female Count + Clutch Size + Lay Date + Male Count * Clutch Size + (Cluster) + (Year)	9	-1241.39	2500.86	1.06	0.12
Site: Sandhills **Brood Loss Type: LPBL**						
	Year + Male Count + Female Count + Clutch Size + Group Density + Floater Count + Lay Date + Male Count * Clutch Size + (Cluster) + (Year)	11	-1194.37	2410.89	0.00	0.38
	Male Count + Female Count + Clutch Size + Floater Count + Year + Lay Date + Male Count * Clutch Size + Male Count * Year + (Cluster) + (Year)	11	-1194.64	2411.43	0.54	0.29
Site: Lejeune **Brood Loss Type: EPBL**						
	Male Count + Female Count + Clutch Size + Group Density + Lay Date + (Cluster) + (Year)	8	-730.16	1476.43	0.00	0.40

	Male Count + Female Count + Clutch Size + Year + Group Density + Lay Date + (Cluster) + (Year)	9	-730.09	1478.30	1.87	0.16
	Group Density + Male Count + Female Count + Clutch Size + Lay Date + Male Count * Clutch Size + (Cluster) + (Year)	9	-730.15	1478.42	1.99	0.15
Site: Lejeune **Brood Loss Type: LPBL**						
	Clutch Size + Adults per Hectare + Floater Count + Lay Date + (Cluster) + (Year)	7	-786.73	1587.55	0.00	0.59
Site: Eglin **Brood Loss Type: EPBL**						
	Clutch Size + Male Count + Female Count + Year + Lay Date + (Cluster) + (Year)	8	-269.59	555.47	0.00	0.18
	Clutch Size + Male Count + Female Count + Lay	7	-270.89	556.00	0.53	0.13

Date + Year + (Cluster) + (Year)					
Clutch Size + Male Count + Female Count + Year + Lay Date + Male Count * Year + (Cluster) + (Year)	9	-269.13	556.63	1.15	0.10
Clutch Size + Male Count + Female Count + Year + Lay Date + Male Count * Eggs + (Cluster) + (Year)	9	-269.18	556.73	1.25	0.09
Male Count + Female Count + Clutch Size + Year + Group Density + Lay Date + (Cluster) + (Year)	9	-269.45	557.26	1.78	0.07

Site: Eglin
Brood Loss Type: LPBL

Clutch Size + Male Count + Female Count + Year + Lay Date + (Cluster) + (Year)	8	-269.59	555.47	0.00	0.18
Clutch Size + Male Count + Female Count + Lay Date + (Cluster) + (Year)	7	-270.89	556.00	0.53	0.14
Clutch Size + Male Count	9	-269.13	556.63	1.15	0.10

+ Female Count + Year + Lay Date + Male Count * Year + (Cluster) + (Year)					
Clutch Size + Male Count + Female Count + Year + Lay Date + Male Count * Clutch Size + (Cluster) + (Year)	9	-269.18	556.73	1.25	0.09
Male Count + Female Count + Clutch Size + Year + Group Density + Lay Date + (Cluster) + (Year)	9	-269.45	557.26	1.78	0.07

Table B.5. Model-averaged standardized coefficient estimates for predictors influencing the occurrence of early and late partial brood loss (EPBL and LPBL) at Sandhills, Lejeune, and Eglin.

Predictor	Estimate	Std-Error	Adjusted_SE	Z_value	P-value	Lower CI	Upper CI
Site: Sandhills **Brood Loss Type: EPBL**							
Intercept	0.84	0.07	0.07	11.49	0.00	0.69	0.98
Male Count	-0.52	0.05	0.05	9.37	0.00	-0.63	-0.41
Female Count	-0.01	0.05	0.05	0.26	0.78	-0.11	0.08
Clutch Size	1.02	0.06	0.06	16.38	0.00	0.90	1.15
Year	-0.00	0.06	0.06	0.02	0.98	-0.12	0.11
Group Density	-0.04	0.05	0.05	0.70	0.48	-0.15	0.07
Lay Date	0.38	0.05	0.05	6.48	0.00	0.26	0.49
Clutch Size * Male Count	-0.14	0.06	0.06	2.25	0.02	-0.26	-0.01
Male Count * Year	0.07	0.07	0.07	0.98	0.32	-0.07	0.22
Floater Count	-0.01	0.03	0.03	0.44	0.65	-0.09	0.05
Clutch Size * Female Count	-0.00	0.00	0.00	0.00	0.99	-0.01	0.01
Adults per Hectare	-0.00	0.00	0.00	0.00	1.00	-0.00	-0.00
Adults per Hectare * Clutch Size	0.00	0.00	0.00	0.00	1.00	-0.00	0.00
Site: Sandhills **Brood Loss Type: LPBL**							
Intercept	-0.60	0.07	0.07	8.45	0.00	-0.74	-0.46

Year	0.29	0.07	0.07	4.15	0.00	0.15	0.43
Male Count	-0.15	0.07	0.07	2.09	0.03	-0.29	-0.00
Female Count	-0.00	0.04	0.04	0.00	0.99	-0.09	0.09
Clutch Size	0.24	0.05	0.05	4.52	0.00	0.13	0.35
Group Density	-0.01	0.04	0.04	0.43	0.66	-0.09	0.06
Floater Count	0.11	0.06	0.06	1.73	0.08	-0.01	0.24
Lay Date	0.34	0.05	0.05	6.30	0.00	0.23	0.45
Clutch Size * Male Count	0.07	0.06	0.06	1.22	0.21	-0.04	0.19
Male Count * Year	-0.00	0.03	0.03	0.04	0.96	-0.07	0.07
Female Count * Year	-0.00	0.02	0.02	0.10	0.91	-0.04	0.03
Clutch Size * Female Count	0.00	0.00	0.00	0.10	0.91	-0.01	0.02
Adults per Hectare	-0.00	0.01	0.01	0.12	0.90	-0.02	0.02
Adults per Hectare * Clutch Size	0.00	0.01	0.01	0.10	0.91	-0.02	0.02
Site: Lejeune **Brood Loss Type: EPBL**							
Intercept	1.22	0.08	0.08	14.35	0.00	1.06	1.39
Male Count	-0.45	0.07	0.07	6.43	0.00	-0.59	-0.31
Female Count	-0.08	0.06	0.06	1.27	0.20	-0.21	0.04
Clutch Size	1.18	0.08	0.08	14.14	0.00	1.02	1.34
Group Density	-0.17	0.09	0.09	1.95	0.05	-0.35	0.00
Lay Date	0.14	0.07	0.07	2.03	0.04	0.00	0.28
Year	-0.01	0.04	0.04	0.25	0.80	-0.10	0.08
Clutch Size * Male Count	0.00	0.04	0.04	0.09	0.92	-0.07	0.08
Male Count * Year	-0.00	0.02	0.02	0.13	0.89	-0.05	0.04
Floater Count	0.00	0.02	0.02	0.17	0.86	-0.04	0.05

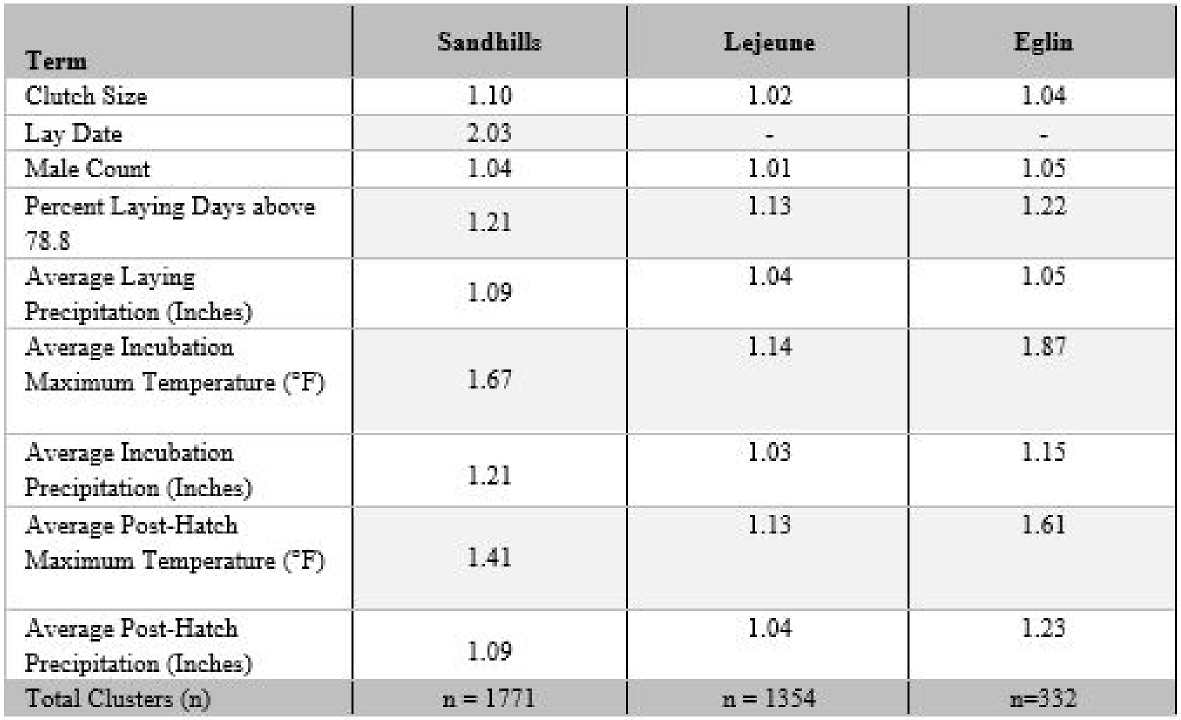
Clutch Size * Female Count	0.00	0.00	0.00	0.05	0.95	-0.01	0.01
Adults per Hectare	-0.00	0.00	0.00	0.00	0.99	-0.00	0.00
Adults per Hectare * Clutch Size	0.00	0.00	0.00	0.00	0.99	-0.00	0.00
Site: Lejeune **Brood Loss Type: LPBL**							
Intercept	-0.62	0.07	0.07	8.69	0.00	-0.76	-0.48
Clutch Size	0.25	0.06	0.06	3.82	0.00	0.12	0.37
Adults per Hectare	-0.17	0.13	0.13	1.35	0.17	-0.43	0.07
Floater Count	0.07	0.06	0.06	1.08	0.27	-0.05	0.20
Lay Date	0.00	0.06	0.06	0.02	0.97	-0.12	0.12
Group Density	0.04	0.07	0.07	0.55	0.57	-0.10	0.18
Male Count	-0.05	0.09	0.09	0.59	0.55	-0.24	0.13
Female Count	-0.01	0.04	0.04	0.35	0.72	-0.09	0.06
Year	0.00	0.03	0.03	0.17	0.85	-0.06	0.07
Adults per Hectare * Clutch Size	-0.00	0.02	0.02	0.09	0.92	-0.04	0.04
Male Count * Year	-0.00	0.02	0.02	0.20	0.83	-0.06	0.05
Clutch Size * Male Count	-0.00	0.01	0.01	0.00	0.99	-0.03	0.03
Female Count * Year	-0.00	0.00	0.00	0.03	0.96	-0.01	0.01
Clutch Size * Female Count	0.00	0.00	0.00	0.01	0.98	-0.00	0.00
Site: Eglin **Brood Loss Type: EPBL**							

	Intercept	0.96	0.11	0.11	8.38	0.00	0.73	1.18
	Clutch Size	1.08	0.13	0.13	8.05	0.00	0.82	1.34
	Male Count	-0.43	0.11	0.11	3.89	0.00	-0.65	-0.21
	Female Count	-0.14	0.10	0.10	1.36	0.17	-0.36	0.06
	Year	0.19	0.11	0.11	1.62	0.10	-0.04	0.42
	Lay Date	0.17	0.12	0.12	1.42	0.15	-0.06	0.41
	Male Count * Year	0.10	0.11	0.11	0.94	0.34	-0.11	0.32
	Clutch Size * Male Count	0.13	0.14	0.14	0.87	0.37	-0.16	0.42
	Group Density	-0.05	0.10	0.10	0.53	0.59	-0.27	0.15
Site: Eglin **Brood Loss Type: LPBL**								
	Intercept	-0.39	0.10	0.11	3.62	0.00	-0.61	-0.18
	Female Count	-0.25	0.11	0.11	2.11	0.03	-0.48	-0.01
	Lay Date	-0.01	0.12	0.12	0.08	0.93	-0.24	0.22
	Clutch Size	0.17	0.11	0.11	1.51	0.13	-0.05	0.39
	Male Count	-0.09	0.11	0.11	0.82	0.40	-0.32	0.13
	Year	0.10	0.12	0.12	0.84	0.40	-0.14	0.36
	Clutch Size * Male Count	0.21	0.11	0.12	1.77	0.07	-0.02	0.44
	Male Count * Year	-0.15	0.11	0.11	1.27	0.20	-0.38	0.08
	Group Density	-0.06	0.10	0.10	0.57	0.56	-0.27	0.15

Table C.1. Summary statistics for climatic influence on the occurrence of early partial brood loss for Sandhills, Lejeune, and Eglin.

	Sandhills						Lejeune						Eglin					
	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max
Continuous																		
Clutch Size	2	3	4	3	4	5	2	3	4	3	4	5	2	3	3	3	3	5
Male Count	0	1	2	1	2	5	0	1	2	1	2	6	0	1	2	1	2	5
Attempt Group	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	2
Lay Date	101	116	122	123	129	170	99	118	123	123	127	158	97	117	124	124	131	160
Percent of Laying Days above 78.8 (°F)	0	25	50	55.03	100	100	0	0	0	30.62	50	100	0	66.66	100	78.71	100	100
Average Laying Precipitation (Inches)	0	0	0.02	0.10	0.13	1.02	0	0	0	0.12	0.06	3.38	0	0	0	0.12	0.15	1.67
Average Incubation Maximum Temperature (°F)	61.94	76.42	79.53	79.54	82.81	96.77	61.93	73.74	76.46	76.54	79.20	92.37	75.82	80.87	83.84	83.90	86.36	96.93
Average Incubation Precipitation (Inches)	0	0.02	0.07	0.10	0.16	0.86	0	0.01	0.07	0.11	0.18	1.99	0	0.01	0.08	0.15	0.22	1.37
Average Post-Hatch Maximum Temperature (°F)	65.09	77.85	81.28	81.27	84.48	97.87	59.10	74.76	77.85	77.84	80.81	97.63	75.38	80.07	86.20	86.42	88.38	99.31
Average Post-Hatch Precipitation (Inches)	0	0.01	0.05	0.10	0.13	1.63	0	0.06	0.06	0.14	0.18	2.57	0	0.02	0.11	0.16	0.25	2.98
Categorical																		
Year	1981	1998	2009	2006	2016	2023	1986	2002	2010	2008	2017	2022	1995	2008	2013	2012	2018	2023

Table C.2. Variance Inflation Factor (VIF) summary among variables for the climatic influence on the occurrence of early partial brood loss for Sandhills, Lejeune, and Eglin.



Term	Sandhills	Lejeune	Eglin
Clutch Size	1.10	1.02	1.04
Lay Date	2.03	-	-
Male Count	1.04	1.01	1.05
Percent Laying Days above 78.8	1.21	1.13	1.22
Average Laying Precipitation (Inches)	1.09	1.04	1.05
Average Incubation Maximum Temperature (°F)	1.67	1.14	1.87
Average Incubation Precipitation (Inches)	1.21	1.03	1.15
Average Post-Hatch Maximum Temperature (°F)	1.41	1.13	1.61
Average Post-Hatch Precipitation (Inches)	1.09	1.04	1.23
Total Clusters (n)	n = 1771	n = 1354	n=332

Table C.3. Model summaries for climatic influence on the occurrence of early partial brood loss across Sandhills, Lejeune, and Eglin. The best-supported model (lowest ΔAICc) is shown in bold.

Site	Model Description	K (df)	-2LogLik	AIC_c	ΔAIC_c	w
Sandhills	**Clutch Size + Male Count + Attempt Group + Average Post-Hatch Maximum Temperature + Average Post-Hatch Precipitation**	**10**	**-3685.99**	**7392.02**	**0.00**	**0.93**
Sandhills	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation + Average Incubation Maximum Temperature + Average Incubation Precipitation + Average Post-Hatch Maximum Temperature + Average Post-Hatch Precipitation	14	-3685.10	7398.28	6.26	0.04
Sandhills	Clutch Size + Male Count + Attempt Group + Average Incubation Maximum Temperature + Average Incubation Precipitation	10	-3690.43	7400.91	8.89	0.01

Sandhills	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation	10	-3690.50	7401.04	9.01	0.01
Sandhills	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation + Average Incubation Maximum Temperature + Average Incubation Precipitation	12	-3689.36	7402.77	10.75	0.00
Lejeune	**Clutch Size + Male Count + Attempt Group + Average Post-Hatch Maximum Temperature + Average Post-Hatch Precipitation**	**10**	**-3044.78**	**6109.61**	**0.00**	**1**
Lejeune	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation	10	-3045.93	6111.91	2.29	0.19
Lejeune	Clutch Size + Male Count + Attempt Group + Average Incubation Maximum Temperature + Average Incubation Precipitation	10	-3046.14	6112.33	2.71	0.15

Lejeune	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation + Average Incubation Maximum Temperature + Average Incubation Precipitation	12	-3045.93	6115.93	6.31	0.02
Lejeune	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation + Average Incubation Maximum Temperature + Average Incubation Precipitation + Average Post-Hatch Maximum Temperature + Average Post-Hatch Precipitation	14	-3044.29	6116.67	7.05	0.01
Eglin	**Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation**	**10**	**-672.29**	**1364.80**	**0.00**	**0.32**

Eglin	Clutch Size + Male Count + Attempt Group + Average Incubation Maximum Temperature + Average Incubation Precipitation	10	-672.50	1365.21	0.41	0.26
Eglin	Clutch Size + Male Count + Attempt Group + Average Post-Hatch Maximum Temperature + Average Post-Hatch Precipitation	10	-672.51	1365.24	0.43	0.25
Eglin	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation + Average Incubation Maximum Temperature + Average Incubation Precipitation	12	-672.08	1366.46	1.65	0.13

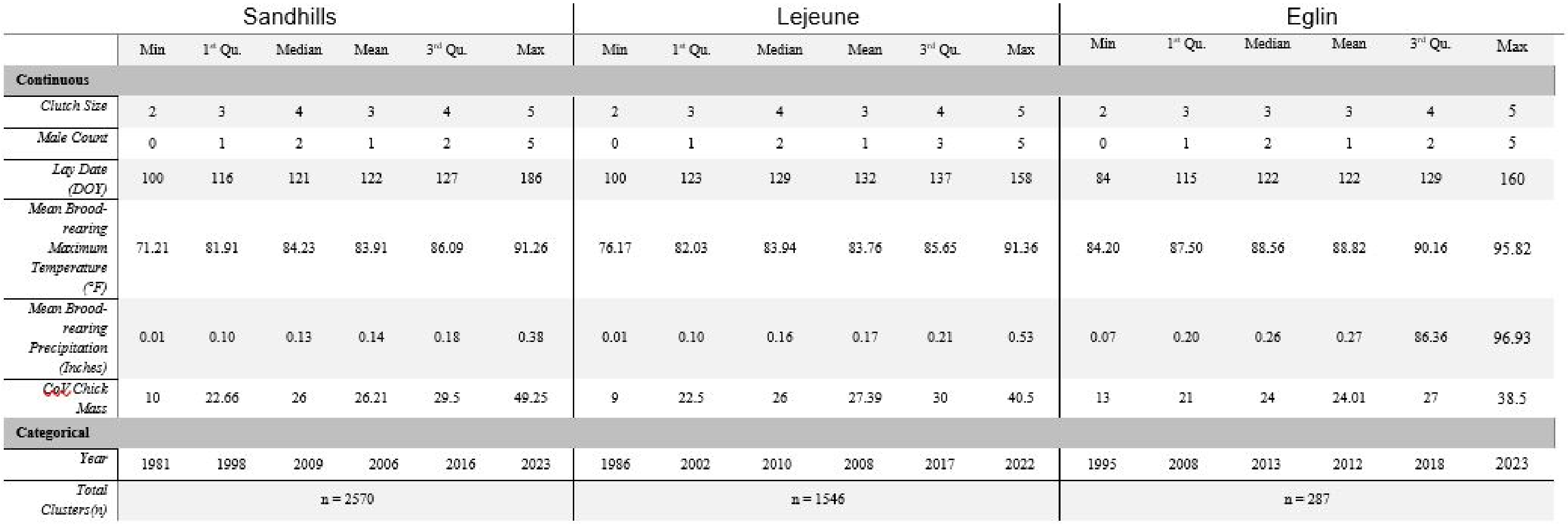
Eglin	Clutch Size + Male Count + Attempt Group + Percent Laying Days above 78.8 + Average Laying Precipitation + Average Incubation Maximum Temperature + Average Incubation Precipitation + Average Post-Hatch Maximum Temperature + Average Post-Hatch Precipitation	14	-672.91	1370.23	5.42	0.02

Table C.4. Standardized coefficient estimates from top model of predictors for climatic influence on the occurrence of early partial brood loss for Sandhills, Lejeune, and Eglin.

Site	Model	Predictor	Estimate	Std-Error	Z_value	P-value	Lower CI	Upper CI
Sandhills	Model 5	Clutch Size	0.05	0.00	9.38	0.00	0.04	0.06
Sandhills		Male Count	-0.05	0.00	-9.03	0.00	-0.06	-0.03
Sandhills		Attempt Group	0.03	0.00	5.24	0.00	0.01	0.04
Sandhills		Average Post-Hatch Maximum Temperature	0.01	0.00	3.36	0.00	0.00	0.03
Sandhills		Average Post-Hatch Precipitation	-0.00	0.00	-0.03	0.97	-0.01	0.01
Lejeune	Model 5	Clutch Size	0.06	0.00	10.19	0.00	0.05	0.07
Lejeune		Male Count	-0.04	0.00	-6.55	0.00	-0.05	-0.02
Lejeune		Attempt Group	0.00	0.00	0.24	0.80	-0.01	0.01

Lejeune		Average Post-Hatch Maximum Temperature	-0.00	0.00	-1.46	0.14	-0.02	0.00
Lejeune		Average Post-Hatch Precipitation	0.00	0.00	0.67	0.50	-0.00	0.01
Eglin	Model 2	Clutch Size	0.07	0.01	5.63	0.00	0.05	0.10
Eglin		Male Count	-0.02	0.01	-1.43	0.15	-0.05	0.00
Eglin		Attempt Group	0.01	0.01	0.80	0.42	-0.01	0.03
Eglin		Percent Laying Days above 78.8	-0.00	0.01	-0.50	0.61	-0.03	0.02
Eglin		Average Laying Precipitation	0.01	0.01	1.16	0.24	-0.01	0.05

D.1. Summary statistics for chick size and weather conditions on the occurrence of late partial brood loss for Sandhills, Lejeune, and Eglin.



	Sandhills						Lejeune						Eglin					
	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max	Min	1st Qu.	Median	Mean	3rd Qu.	Max
Continuous																		
Clutch Size	2	3	4	3	4	5	2	3	4	3	4	5	2	3	3	3	4	5
Male Count	0	1	2	1	2	5	0	1	2	1	3	5	0	1	2	1	2	5
Lay Date (DOY)	100	116	121	122	127	186	100	123	129	132	137	158	84	115	122	122	129	160
Mean Brood-rearing Maximum Temperature (°F)	71.21	81.91	84.23	83.91	86.09	91.26	76.17	82.03	83.94	83.76	85.65	91.36	84.20	87.50	88.56	88.82	90.16	95.82
Mean Brood-rearing Precipitation (Inches)	0.01	0.10	0.13	0.14	0.18	0.38	0.01	0.10	0.16	0.17	0.21	0.53	0.07	0.20	0.26	0.27	86.36	96.93
CoV Chick Mass	10	22.66	26	26.21	29.5	49.25	9	22.5	26	27.39	30	40.5	13	21	24	24.01	27	38.5
Categorical																		
Year	1981	1998	2009	2006	2016	2023	1986	2002	2010	2008	2017	2022	1995	2008	2013	2012	2018	2023
Total Clusters (n)	n = 2570						n = 1546						n = 287					