The Influence of Nest Structure and Location on Nesting Success and Nest Microclimate of Native Landbirds in Grenada

by

Zahra Nanji

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Natural Resources Institute
Clayton H. Riddell Faculty of Environment, Earth, and Resources
University of Manitoba
Winnipeg, MB

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Abstract

In Grenada, habitat loss and introduced predators pose significant immediate threats to resident landbirds, while climate warming and the associated rise in climate-related disturbances are increasingly pressing and may compound these existing threats. These pressures may alter the availability and quality of suitable nesting sites and, in turn, reshape nesting strategies and reproductive outcomes in resident landbird populations. Despite these pressures, little is known about how nest architecture and nest-site characteristics influence nesting success in Grenada's landbirds. This study evaluated ecological drivers of nesting success and variation in nest microclimate among 11 resident landbirds with open-cup and enclosed nesting strategies. Research was conducted at Belmont Estate during two field seasons (2023 and 2025). In 2023, 70 nests were monitored to assess the effects of nest type, microhabitat characteristics, Site, and seasonal timing on nesting success. In 2025, we used iButton temperature sensors to collect paired internal and ambient temperature measurements from 13 nests representing five species to assess variation in nest microclimate.

Logistic-exposure modelling from 2023 revealed that open-cup nests had higher estimated daily survival than enclosed nests (98.7% vs. 96.6%), corresponding to cumulative survival probabilities of 69.1% and 36.9%, respectively. Open-cup nests exhibited approximately 2.7 times the odds of daily survival. A strong positive interaction between nest height and nest type was identified, with survival increasing substantially with height among open-cup nests but changing comparatively little among enclosed nests. Greater canopy density was associated with reduced survival among open-cup nests, whereas its effect was weak among enclosed nests.

In 2025, generalized additive mixed-model and generalized least-squares analyses found that nest microclimate remained closely coupled to ambient conditions and did not consistently differ across nest architectures. Descriptive patterns nevertheless suggested that the thermal relationship between nest architectures varied across reproductive stages, with open-cup nests exhibiting a greater positive thermal offset during the nestling stage. Although this difference approached 3.5°C, considerable uncertainty limits population-level inference.

These findings demonstrate that the ecological consequences of nest architecture in Grenada are context-dependent. Ultimately, this study represents an important step toward understanding which nesting strategies may be most vulnerable or resilient to changing environmental conditions and provides a baseline for future research examining how climate warming, habitat alteration, and shifting predator pressures may influence nesting strategies and reproductive success in Grenada.

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Chapter 1: Introduction

1.1 Background

Birds are essential to ecosystem resilience, providing vital services such as pollination, seed dispersal, pest control, and nutrient cycling (Gaston, 2022; Whelan et al., 2008). They are critical to maintaining ecosystem functions, biodiversity, and structural integrity. Importantly, due to their broad geographic distribution and sensitivity to environmental changes, birds serve as excellent environmental indicators, providing valuable insights into ecosystem state and change (Bibby, 1999; Hutto, 1998; Şekercioğlu et al., 2025). However, global avian populations are declining at unprecedented rates due to anthropogenic and natural disturbances, resulting in habitat loss, habitat fragmentation, and increased pressure from invasive species (Betts et al., 2022; Doherty et al., 2016; Lees et al., 2022). Ultimately, declines in avian populations can lead to cascading ecological consequences and disrupt these vital ecosystem processes (Şekercioğlu et al., 2025; Weeks et al., 2026).

Understanding avian reproductive strategies and the factors that influence nesting success is essential for interpreting ecological information from bird populations, helping us detect early environmental changes and prevent potential catastrophic collapses (Bibby, 1999; Hutto, 1998; Şekercioğlu et al., 2025). This is especially important for resident avifauna populations on oceanic islands, which are vulnerable and sensitive to ecosystem changes because of their geographic isolation, limited evolutionary exposure to novel stressors, and limited land area (MacArthur, 1968; MacArthur & Wilson, 1967). Island avifauna therefore often have lower species richness and limited gene flow because restricted recolonization opportunities reduce

their capacity to recover from disturbance events and increase their risk of species extinction (Ando, 2019; Frankham, 1997; MacArthur & Wilson, 1967).

In the Caribbean, a region characterized by intense solar radiation, tropical storms with extreme precipitation, high humidity, and high temperatures, these vulnerabilities are exacerbated by anthropogenic and climate-related disturbances (Di Napoli et al., 2023; Sircar et al., 2024). Situated on the front lines of the global climate crisis, these islands face intensifying hurricanes that cause extensive loss of critical habitat on which resident birds rely (Cavallo et al., 2023; Li et al., 2026; Wiley & Wunderle, 1993). Although Caribbean Small Island Developing States (SIDS) contribute less than 1% of global greenhouse gas emissions, they are disproportionately affected by these disruptions (Cavallo et al., 2023; Wiley & Wunderle, 1993). Furthermore, despite the region's status as a global biodiversity hotspot, resident birds remain understudied compared with temperate or migratory populations. This temperate bias in ornithology impedes understanding of the breeding ecology of tropical resident birds and their responses to environmental change and increased pressures from invasive predators, creating a significant knowledge gap (de Lima et al., 2011; Latta, 2012; Lees et al., 2020).

In the Lesser Antilles, particularly Grenada, this knowledge gap is especially pronounced. Grenada is a small oceanic island (~348 kn²) in the southern Caribbean characterized by a mosaic of secondary forest, agricultural land, and developed areas (Groome, 1970). Historical agricultural conversion, ongoing urbanization and tourism development, and repeated climate-related disturbances such as hurricanes have substantially altered the island’s habitat structure and reduced ecosystem resilience (Government of Grenada, 2014; Gould et al., 2020; Hay, 2013; UNEP, 2014). As a Small Island Developing State (SIDS), Grenada is particularly vulnerable to

these pressures, including habitat loss and fragmentation, drought, hurricanes, and sea-level rise (Briguglio, 1995; Gould et al., 2020; Government of Grenada, 2014; UNEP, 2014). These repeated environmental pressures and disturbance events may significantly influence nesting success because it alters nesting strategies and reproductive outcomes in resident bird populations due to reduced availability off breeding and foraging habitat, altering the availability and quality of nest sites, and modifying predator abundance and access to active nests (Chiavacci et al., 2018; Doherty et al., 2016; Reynolds et al., 2019; Wiley & Wunderle, 1993).

Although recent studies have improved our understanding of species distributions, densities, and behaviour of some of Grenada's resident landbirds, there remains a critical lack of information on the ecological mechanisms that influence population viability, particularly those related to reproduction and nesting success (De Ruyck, 2023; Devenish-Nelson & Nelson, 2021; Heathcote et al., 2021; Williams et al., 2023). Abundance alone is often a misleading indicator of habitat quality, as high densities may occur in ecological traps where individuals are attracted to habitats that ultimately result in low reproductive success (Battin, 2004; Van Horne, 1983). Quantifying nesting success provides a far more sensitive measure of demographic performance (Bailey et al., 2019; Johnson, 1979). Understanding these drivers is essential for ensuring the long-term viability of Grenada’s native resident avifauna.

Nest predation is a key selective pressure shaping avian reproductive success and a major driver of reproductive failure in birds (Ibáñez-Álamo et al., 2015; Martin, 1995; Menezes & Marini, 2017). While predation is a fundamental ecological process that regulates prey populations, invasive species can disrupt established predator–prey dynamics and introduce novel sources of mortality (Blackburn et al., 2004; Doherty et al., 2016). For this reason,

invasive species are recognized as one of the greatest threats to biodiversity worldwide (Blackburn et al., 2004; Trouwborst et al., 2020).

Historically, predation pressure in Grenada was likely concentrated in the arboreal and aerial strata, dominated by natural predators such as the Grenada Tree Boa (*Corallus grenadensis*), the Antillean Broad-winged Hawk (*Buteo platypterus antillarum*), and the Lesser Antillean Barn Owl (*Tyto insularis nigrescens*) (Campbell et al., 2022; Heathcote et al., 2021; Henderson & Berg, 2011; Jiang, 2018). However, the introduction of invasive mammalian predators, including the small Indian mongoose (*Urva auropunctata*), cats (*Felis silvestris catus*), rats (*Rattus rattus, R. norvegicus*), and dogs (*Canis lupus familiaris*), substantially altered predator-prey dynamics by introducing new predation pressures, particularly in the ground and lower vegetation strata (Choudhary et al., 2013; Duron et al., 2017; Horst et al., 2001; Hughes & Macdonald, 2013; Medina et al., 2011; Pearson, 2009; Trouwborst et al., 2020; Zieger et al., 2014). These novel predation pressures, combined with ongoing habitat modification, could significantly affect nest vulnerability and reproductive success in Grenada's avifauna (Blackburn et al., 2004; Case & Bolger, 1991).

1.1.1 Nest Type Functions

Grenada's native landbirds exhibit a range of nesting strategies, including both open-cup and enclosed nest architectures. Nests are a key resource for population persistence, primarily protecting eggs and nestlings from predators and environmental extremes (Deeming & Mainwaring, 2015; De Zwaan et al., 2020; Mainwaring et al., 2014). Enclosed nests were traditionally regarded as an adaptation to increased predation, owing to their structural capacity

to conceal nest contents compared with the simpler, more exposed open-cup nest (Skutch, 1985; Snow & Snow, 1963). However, recent evolutionary evidence indicates that enclosed nesting is ancestral in passerines, with open-cup nesting evolving repeatedly through the loss of enclosed nest architecture over evolutionary time (Medina, 2019; Medina et al., 2022; Price & Griffith, 2017). This suggests that nest architecture reflects trade-offs among multiple selective pressures rather than serving solely to protect against predators.

The exposed nature of open nests gives nesting adults an unobstructed view of approaching threats and multiple escape routes. This, in turn, can enable earlier detection of predators than in enclosed nests, which have only one narrow entry and exit point. Further, the simpler structure of open-cup nests requires fewer construction materials and less time, reducing energy demands (Mainwaring et al., 2014; Martin et al., 2017). These nests are also typically built by larger-bodied species and, as such, require more stable, supportive substrates to accommodate both adult and developing brood mass, potentially restricting placement to structurally suitable sites (Biddle et al., 2018; Hansell, 2000). In contrast, enclosed nests, typically built by smaller-bodied species, may attach to a wider range of substrates because their woven or suspended designs allow them to be supported by more flexible vegetation (Hansell, 2000; Sheard et al., 2024). Enclosed nests may also provide greater protection of nest contents from environmental extremes, including heavy rainfall, wind, and intense solar radiation (Collias & Collias, 2014; Martin et al., 2017). However, the trade-off is that enclosed nests are generally more structurally complex and larger relative to the builder's body size than open-cup nests and, as such, require greater investments of time, materials, and energy during construction

(Mainwaring et al., 2014; Taylor et al., 2024). Additionally, although their enclosed architecture can conceal eggs and nestlings, the larger physical structure of an enclosed nest may itself be more conspicuous to visual predators (Ibáñez-Álamo et al., 2015; Martin, 1993a, 1993b). Together, these contrasting characteristics between nest types represent fundamental trade-offs among concealment of nest contents, predator detection and escape, physical stability, energetic costs, and protection from environmental extremes (Mainwaring et al., 2014; Vanadzina et al., 2024).

1.1.2 Nest-site Selection and the Microhabitat

Nest-site selection is a critical component of avian reproductive strategy and is influenced by both predation pressure and environmental conditions. Birds must therefore select sites that balance predator protection with the nest's thermoregulatory demands (Borgmann & Conway, 2015; Harris & McMurry, 2024; Ibáñez-Álamo et al., 2015; Latif et al., 2012; Ricklefs, 1969; Sheard et al., 2024). In hot environments, this can involve selecting sites sheltered from environmental extremes to reduce the risk of overheating (Mainwaring et al., 2014). Nest-site quality depends on the nest type and surrounding microhabitat characteristics, such as concealment, nest height, and nesting substrate, because placement must accommodate the nest's structural requirements. Open-cup nests may require relatively stable and supportive substrates, such as palm fronds, thick, sturdy branches on trees, or other robust vegetation, whereas woven enclosed nests may be attached to vines, bushes, anthropogenic structures, or smaller, thinner branches on trees (Hansell, 2000; Sheard et al., 2024). Differences in nest architecture may therefore allow species to exploit different portions of the available nesting environment.

Increased canopy density around a nest can reduce its visibility to predators by concealing both the nest itself and the movements of attending adults. Dense vegetation may also reduce the transmission or detection of nestling begging calls while providing additional protection from environmental extremes (Liu et al., 2021; Martin et al., 2000). Open nests lack structural protection from environmental extremes and may therefore benefit from placement beneath vegetation or other forms of overhead cover (Conway & Martin, 2000; Deeming & Mainwaring, 2015). In contrast, enclosed nests may benefit from greater airflow to facilitate ventilation and drying and, as such, cannot be as concealed by vegetation. The trade-off is that open-cup nests can be tucked into vegetation, whereas enclosed nests cannot be as concealed, making them easier for visual predators to locate.

Nest height introduces an additional trade-off by altering exposure to different predator guilds. Nests in lower strata, closer to the ground, may be more accessible to ground predators, such as invasive mammals like the small Indian mongoose. Conversely, nests higher in the canopy may be more exposed to arboreal or aerial predators, such as the Grenada tree boa and the Lesser Antillean Broad-winged Hawk (Matysioková & Remeš, 2022, 2024). Furthermore, because open-cup and enclosed nests differ in structural requirements and placement opportunities, the relationship between nest height and predation risk may also vary between nest architectures (Altamirano et al., 2019; Chia et al., 2026; Matysioková & Remeš, 2024). Height may also alter nest microclimatic and thermoregulatory demands, as nests at different vertical positions experience variations in solar radiation, vegetation cover, airflow, and other environmental conditions (Deeming & Reynolds, 2015; Tieleman et al., 2004).

Increased pressures from habitat loss, predation, or a warming climate may force Grenada's landbirds to trade off aspects of their preferred nest site, leaving them more vulnerable (Eggers et al., 2006; Mainwaring et al., 2014). Importantly, the relative costs and benefits of a particular nest site are unlikely to remain constant throughout the breeding season, as vegetation structure, predator activity, rainfall, and other environmental conditions fluctuate (Martin, 1998; Skutch, 1985).

1.1.3 Temporal Effects: Seasonality and Breeding Phenology

Tropical systems are characterized by precipitation-driven seasonality, with peak breeding often synchronized with the onset of the rainy season to maximize food availability for adults and developing offspring through seasonal increases in energy-rich resources such as arthropods and fruit (De Ruyck, 2023; Skutch, 1985). In Grenada, peak avian breeding generally occurs from approximately May to July, and many of Grenada's landbirds exhibit more generalist behaviours that enable them to track these seasonal pulses (Devenish-Nelson & Nelson, 2021; De Ruyck, 2023).

Seasonal changes in rainfall and resource availability may similarly influence the abundance, reproductive activity, and energetic demands of potential nest predators. Although many invasive mammalian predators in tropical environments can reproduce over extended periods because of relatively stable temperatures and year-round food availability, their reproductive activity and population dynamics may still vary seasonally (Harper & Bunbury, 2015; Ortega-Pacheco et al., 2012; de Camargo et al., 2021). In Lesser Antillean dry forests, for example, rat reproduction declines during drier periods and increases following the onset of

wetter conditions, while pregnant Small Indian Mongooses have been documented on Grenada throughout much of the year, including during the primary avian breeding period (Goedert et al., 2020; Nellis & Everard, 1983; Zieger et al., 2014). Domestic and feral cats may likewise reproduce throughout much of the year in tropical environments, maintaining the potential for predation throughout the avian breeding season, although reproductive activity may still vary seasonally (Ortega-Pacheco et al., 2012; Medina et al., 2011). Reproductive activity of native predators may also overlap temporally with the avian breeding season. Antillean Broad-winged Hawks (*Buteo platypterus antillarum*) breed approximately from March through July, when energetic demands may increase as adults provision offspring, whereas Grenada tree boas (*Corallus grenadensis*) generally mate during the dry season before giving birth during the wet season (Campbell et al., 2022; Henderson & Berg, 2011). Thus, although the timing and magnitude of seasonal responses differ among predator species, Grenada's peak avian breeding season overlaps with reproductive or energetically demanding periods for several native and invasive predators, potentially contributing to temporal variation in nest predation risk.

Predation risk may also vary throughout the breeding season as nest abundance, vegetation structure, and parental behaviour change over time. Seasonal vegetation growth can increase nest concealment while altering predator movement and detection opportunities (Borgmann & Conway, 2015). During periods of high nesting activity, particularly when a greater proportion of active nests reach the nestling stage, increased parental visitation for provisioning and nest sanitation, together with increased nestling vocalizations, may heighten the visual and auditory cues available to predators and consequently increase nest detectability

(Martin et al., 2000). This mechanism aligns with the Skutch Hypothesis, which proposes that increased parental activity at the nest, particularly during the nestling stage when provisioning rates are high, increases the probability that predators will locate active nests (Skutch, 1949). Predators may therefore respond not only to seasonal changes in their own energetic requirements but also to temporal changes in the abundance and detectability of active nests, potentially increasing predation pressure during periods of high nesting activity (Arslan & Martin, 2024; Martin et al., 2000). Birds, in turn, may respond to heightened predation risk by altering breeding behaviour, including nest-site selection and parental activity (Eggers et al., 2006; Lima, 2009). Together, these processes suggest that nest predation pressure may vary throughout the breeding season because predator biology, prey availability, vegetation landscape, and parental behaviour change concurrently.

1.1.4 Thermoregulation and Nest Microclimate

Alongside predation pressures, Grenada's landbirds must also navigate the challenges imposed by environmental extremes. Tropical species may be particularly susceptible to increasingly extreme temperatures because they often inhabit relatively stable thermal environments and may therefore have narrower thermal tolerances than temperate species exposed to greater climatic variability (DuRant et al., 2019; Janzen, 1967). Enclosed nests are approximately three times more prevalent in tropical ecosystems than at temperate latitudes, a geographic pattern consistent with potential thermoregulatory benefits of enclosed nest architecture at lower latitudes (Martin et al., 2017).

Nest microclimate refers to the abiotic conditions within a nest, including temperature, humidity, and airflow, relative to the surrounding ambient environment (Deeming & Reynolds, 2015). Maintaining suitable microclimatic conditions within the nest is critical for producing viable offspring and, as a result, plays a key role in shaping avian life-history strategies, with consequences for clutch size, developmental periods, and the geographic distribution of nesting strategies (De Zwaan et al., 2020; Mainwaring et al., 2014). Nest structure can modify its internal microclimate through architecture, material composition, and placement, which collectively influence how closely internal conditions track fluctuations in the surrounding environment (Deeming & Mainwaring, 2015; Martin et al., 2017; Price & Griffith, 2017). Enclosed nests, in particular, may help mitigate weather-induced stressors by providing greater insulation and structural protection from extreme environmental conditions (Lamprecht & Schmolz, 2004; Martin et al., 2017; Windsor et al., 2013). This function may be particularly important for altricial nestlings, including those of many Grenadian landbirds, which have limited thermoregulatory capacity during early development and depend strongly on parental care and the internal nest environment to maintain suitable body temperatures for growth and development (Price & Dzialowski, 2018). Notably, thermal conditions within the nest may also vary among reproductive stages as incubation, brooding, nestling metabolism, and parental activity alter heat production and exchange within the nest (Ar & Sidis, 2001; DuRant et al., 2012; Martin, 1993a, 1993b). The degree to which internal nest temperature differs from the surrounding environment can be quantified using thermal offset, defined as the difference between internal nest temperature and ambient temperature (Rhodes et al., 2009). Thermal offset

therefore measures how much nest conditions depart from the external environment and may vary with nest architecture, reproductive stage, time of day, and surrounding microhabitat.

Nest structure and placement may partially mitigate these environmental challenges by influencing solar exposure, airflow, precipitation exposure, and moisture retention within the nest (Deeming, 2002). Open-cup nests are relatively exposed to rainfall and solar radiation but may permit greater air exchange and drying, whereas enclosed nests provide greater structural shelter from precipitation and solar radiation. However, reduced ventilation within enclosed nests may increase heat and moisture retention, particularly under humid tropical conditions, potentially creating conditions favourable to nest deterioration or parasite development (Heenan & Seymour, 2011). These architectural trade-offs may matter most during periods of frequent rainfall and high ambient humidity, when wet nest materials and reduced evaporation can alter the temperature and humidity experienced by eggs and nestlings (Mainwaring et al., 2014; Windsor et al., 2013). Open-cup and enclosed nests may therefore differ in how they modify internal temperatures relative to ambient conditions, with the magnitude and direction of these differences likely to depend on the microhabitat in which the nest is placed (Neel et al., 2021).

These relationships are becoming increasingly relevant in Grenada as rising temperatures throughout the Caribbean increase the potential for heat stress in birds (Coulson et al., 2025). Temperatures in Grenada typically range from about 22°C to 31°C year-round, with extremes approaching 34°C (World Bank Group, 2021). Grenada's mean annual temperature is projected to increase by approximately 0.7-2.6°C by the 2060s, while regional analyses indicate that heat stress has already increased substantially over recent decades (Di Napoli et al., 2023; The Economic Effects of Climate Change in Grenada, 2015). Importantly, extreme heat events tend

to coincide with the rainy season, which also encompasses the peak avian breeding period (Coulson et al., 2025; Ramirez-Beltran et al., 2017). Incubating adults and developing offspring may therefore increasingly encounter combinations of high temperature, humidity, and precipitation during critical reproductive stages, emphasizing the potential importance of nest architecture and placement in modifying the microclimatic conditions experienced by developing eggs and nestlings.

1.1.5 Research Rationale

Birds must navigate trade-offs when selecting nest sites that minimize predation risk while maintaining suitable microclimatic conditions for offspring development. A species' capacity to respond to increased or novel pressures and to manage the associated trade-offs is a key determinant of reproductive success and population outcomes (Mainwaring et al., 2014; Medina et al., 2022; Perez et al., 2023). Identifying the ecological drivers of nesting success is particularly important in systems experiencing rapid environmental and landscape change. In Grenada, habitat loss and introduced predators are immediate threats to resident landbirds, while climate warming and the associated increase in climate-related disturbances are becoming increasingly important pressures that may compound these existing threats. These pressures may alter the availability and quality of suitable nesting sites, and, in turn, reshape nesting strategies and reproductive outcomes in resident landbird populations. Despite these pressures, little is known about how nest architecture and nest-site characteristics influence nesting success in Grenada. It is also unclear whether open-cup and enclosed nests differ in the microclimatic conditions they provide. Addressing these knowledge gaps is important for identifying the

ecological factors associated with successful reproduction and for understanding how species with different nesting strategies may differ in their resilience to the escalating environmental pressures and habitat degradation facing Grenada's unique avian community.

1.1.6 Study Species

This study focused on the most common nesting species in the area (De Ruyck, 2023; Devenish-Nelson & Nelson, 2021; Williams et al., 2023), resulting in the inclusion of 11 focal species representing a range of nesting strategies, habitat associations, and foraging guilds. These comprised 4 enclosed nesters: Bananaquit (*Coereba flaveola aterrima*), Lesser Antillean Bullfinch (*Loxigilla noctis grenadensis*), Grenada Wren (*Troglodytes grenadensis*), and Black-faced Grassquit (*Melanospiza bicolor omissa*), and 7 open-cup nesters: Spectacled Thrush (*Turdus nudigenis nudigenis*), Lesser Antillean Tanager (*Stilpnia cucullata cucullata*), Gray Kingbird (*Tyrannus dominicensis vorax)*, Tropical Mockingbird (*Mimus gilvus antillarum*), Yellow-bellied Elaenia (*Elaenia flavogaster flavogaster*), Common Ground Dove (*Columbina passerina antillarum)*, and Eared Dove (*Zenaida auriculata stenura*). While Passeriformes constitute the island's dominant landbird order, followed by Columbiformes, examining these taxa collectively enables a robust assessment of how differing nest structures (open-cup vs. enclosed) respond to the ecological drivers and environmental stressors previously described.

1.2 Purpose Statement

The primary purpose of this research was to evaluate how nest structure, microhabitat characteristics, and temporal variation influenced the reproductive success of resident landbirds in Grenada. By monitoring nesting success and understanding nest depredation by native and invasive predators, this study aimed to identify the ecological factors that influence avian fitness in a tropical island system.

The secondary purpose of this study was to assess how nest structure, together with nest stage and microhabitat, influenced nest microclimate in open and enclosed nests. By examining thermal offset across distinct nest types, this component aimed to determine the functional significance of nest structure and its potential implications for avian resilience under changing environmental conditions.

1.3 Objectives

Primary objectives: Nesting Success.

1. Evaluate how nest structure (open-cup vs. enclosed), microhabitat characteristics (canopy density and nest height), and seasonal timing affect nesting success among 11 resident landbirds in Grenada.
2. Identify key microhabitat predictors of nest survival to determine how habitat structure mediates predation risk.
3. Describe patterns of nest failure, and document suspected predation events and predator identity (native vs invasive) using observational and trail camera data.

4. Document the general breeding biology and behaviour of the focal species by regularly monitoring and checking active breeding nests.

Secondary objective: Nest Microclimate.

4. Quantify differences in nest microclimate between open-cup and enclosed nests using internal and ambient temperature measurements.
5. Assess how the nest stage (incubation vs. nestling) influences internal nest temperature and thermal offset.
6. Evaluate the influence of microhabitat characteristics (canopy density and nest height) on nest microclimate.
7. Determine how nest type, nest stage and microhabitat interact to influence nest microclimate.

1.4 Hypothesis & Predictions

H1. Nest structure influences nesting success by mediating predator detection and accessibility.

P1.1. Open-cup nests will have higher daily survival than enclosed nests because their exposed architecture provides more opportunities for predator detection and escape**,** whereas enclosed nests will have lower survival because their larger physical structure increases nest-level detectability by visual predators.

H2. Nest height influences nesting success by altering predator exposure.

P2.1. Daily survival will increase with nest height because predator accessibility differs across vertical strata, with lower nests expected to be more vulnerable to invasive terrestrial predators.

P2.2. The effect of nest height on survival will differ between open-cup and enclosed nests because differences in structural requirements and placement opportunities expose the two nest architectures to distinct predator guilds across vertical strata.

H3. **Canopy density influences nesting success by affecting nest concealment.**

P3.1. Nests in areas with greater canopy density will have higher survival due to increased concealment from invasive and native nest predators.

P3.2. Higher canopy density will increase daily survival for open-cup nests more than for enclosed nests because open-cup nests lack structural concealment and therefore rely more heavily on surrounding vegetation for protection against visual detection.

H4. Nesting success varies across the breeding season due to temporal changes in resource availability, vegetation density, predator activity, and parental behaviour.

P4.1. Daily survival will decrease during periods of peak avian breeding activity, when increased nest abundance and parental activity overlap with periods of elevated reproductive and energetic demands among native and invasive predators.

P4.2. The relationship between seasonal timing and daily survival will differ between open-cup and enclosed nests because differences in nest architecture will alter detectability as parental activity increases during periods of high nestling provisioning.

H5 Nest microclimate varies as a function of nest structure, nest stage, and microhabitat characteristics.

P5.1. Thermal offset will differ between nest types, with enclosed nests expected to show greater differences between internal and ambient temperatures than open-cup nests.

P5.2. Nest microclimate will vary across nest stages, with internal temperatures expected to increase during the nestling stage due to increased metabolic heat production.

P5.3. Microhabitat characteristics (canopy density, nest height) will influence the nest microclimate by altering exposure to environmental stressors.

P5.4. Nest microclimate will follow the ambient temperature patterns over a 24-hour period.

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Chapter 2. Literature Review

Understanding the ecological mechanisms that affect nesting success is essential for interpreting patterns in Grenada's native landbird populations and for identifying the drivers of these changes. This chapter provides a more detailed examination of the literature on the study's core topics, offering context for its background and rationale. It will also enhance understanding of the results and future directions. It reviews key ecological processes shaping avian reproductive success, focusing on nest structure, microclimate, nest-site selection, and predation in tropical island systems. It then examines how these factors interact in Grenada, providing context for interpreting patterns of nesting success and microclimatic variation observed in this study.

2.1 Nest Form and Function

The primary function of a nest is to support offspring rearing by providing safety from predators and a stable microclimate for developing eggs and young (De Zwaan et al., 2020; Mainwaring et al., 2014). Nest structure varies widely among species and reflects adaptations to both biotic and abiotic selective pressures, including predation risk, climate, and habitat structure (Price & Griffith, 2017). Variation in nest architecture can, therefore, provide insight into reproductive strategies and constraints across species (Price & Griffith, 2017). Nest materials and design can provide information about the builder's fitness and reproductive investment (Deeming, 2002; Deeming & Mainwaring, 2015).

The types of nests built depend on evolutionary histories and adaptations to environmental pressures (Mainwaring et al., 2014; Martin et al., 2017; Price & Griffith, 2017).

Nest structures can be broadly classified into three main types, each with its own subgroups: (1) Open nest type: scrape, platform, cup. (2) Enclosed nest type: simple dome, complex dome with tunnel, and (3) Cavity nest type: excavation, cavity modifier, excavator-with-nest (Fang et al., 2018; Sheard et al., 2024). This review focuses on open-cup and enclosed nest types, which represent the dominant nesting strategies among the species examined in this study (9 passerines and 2 columbines).

2.1.1 Evolutionary Drivers of Nest Type

Passeriformes, the largest avian order, comprising over 6,000 species and approximately 60% of all bird species worldwide (Clements et al., 2025), exhibit remarkable diversity in nest-building behaviour. This diversity has facilitated extensive adaptive radiation, enabling species to occupy a wide range of ecological niches and terrestrial habitats (Fang et al., 2018; Medina et al., 2022; Price & Griffith, 2017). Among passerines, open-cup nests are the most common and are more prevalent in temperate regions, whereas enclosed (domed) nests are more frequent in tropical and Southern Hemisphere systems (Mainwaring et al., 2014; Martin et al., 2017). This global pattern suggests that nest architecture reflects adaptation to region-specific ecological pressures.

Predation has historically been considered a primary selective force influencing nest form, as nest structure affects both visibility and accessibility to predators (Collias, 1964; Skutch, 1985). However, growing evidence indicates that nest architecture reflects trade-offs among multiple pressures, including predation risk, energetic investment, and environmental conditions

(Jezierski et al., 2025; Mainwaring et al., 2014). Rather than a single driving factor, nest structure represents a balance among competing constraints.

Open-cup nests are typically smaller and require fewer materials, reducing construction time and energetic costs (Martin et al., 2017; Price & Griffith, 2017). Shorter construction periods may also reduce parental activity near the nest, potentially lowering the likelihood of predator detection. In addition, the open structure provides greater visibility and multiple escape routes for attending adults. However, these nests are more exposed to environmental conditions and may be more vulnerable to visually oriented predators. In contrast, enclosed nests are larger and more structurally complex, requiring greater energetic investment and longer construction periods (Taylor et al., 2024). While these nests can protect against environmental stressors such as solar radiation, wind, and precipitation, their size and structure may increase detectability. In particular, enclosed nests may interact differently with predator sensory systems. Although traditionally assumed to dampen sound, recent studies suggest that their structure can channel and amplify nestling begging calls, potentially increasing detectability by acoustically oriented predators (Arslan & Martin, 2024; Mouton & Martin, 2019). In contrast, open-cup nests may disperse sound more widely, making it harder for predators to localize the source.

These contrasting features highlight that nest architecture reflects trade-offs rather than a universally optimal strategy. Despite potential protective benefits, enclosed nests do not consistently reduce predation risk, and open-cup nests remain the most common nest type globally. This suggests that birds may respond more flexibly to predation risk through nest placement and behaviour than through structural changes alone (Briskie et al., 1999; Latif et al., 2012). The higher prevalence of enclosed nests in tropical systems further indicates that their

function likely extends beyond predator avoidance, potentially providing advantages related to environmental conditions, such as temperature and moisture regulation (Collias & Collias, 1959; Martin et al., 2017). These dynamics are particularly relevant in systems such as Grenada, where predator communities and environmental conditions may interact to shape nesting strategies.

2.1.2 Nest Microclimate

The developmental period within the nest is a critical stage for avian reproductive success, during which eggs and nestlings are highly sensitive to environmental conditions (Deeming, 2002; Martin et al., 2007). In altricial species, nestlings are poikilothermic during the early nestling stage. Their body temperature closely tracks ambient temperature and is therefore strongly influenced by environmental conditions. Consequently, altricial nestlings have a thermoregulatory deficit and rely entirely on their parent and the nest to maintain homeostasis until they can do so themselves. Thermoregulatory capacity develops progressively during the early nestling period, although the timing of the transition varies among species (Engert et al., 2025). As a result, early developmental stages are particularly vulnerable to fluctuations in temperature, which can affect growth, physiological development, and survival (De Zwaan et al., 2020; Madden et al., 2026). As endotherms, birds operate within a relatively narrow thermoneutral zone (TNZ), outside which metabolic costs increase to maintain homeostasis (Withers et al., 2016). Exposure to temperatures above the upper critical temperature (UCT) or below the lower critical temperature (LCT) can increase energetic demands, reduce parental efficiency, and compromise offspring development.

Birds inhabiting humid tropical environments may be particularly vulnerable to thermal stress because high air temperatures often coincide with high atmospheric humidity (Di Napoli et al., 2023). As ambient temperature approaches avian body temperature, birds increasingly rely on evaporative heat loss to dissipate metabolic heat (Gerson et al., 2014; Tieleman et al., 2004). Elevated humidity reduces the efficiency of evaporation, thereby limiting thermoregulatory capacity and increasing the risk of heat stress during hot conditions (Coulson et al., 2025; Freeman et al., 2024; Porter et al., 2024). These constraints may be especially important in lowland tropical and subtropical environments, where maximum air temperatures can approach normothermic avian body temperatures while atmospheric humidity remains high (Coulson et al., 2025). For nest-bound eggs and young, which have little or no ability to relocate in response to unfavourable conditions, the physical characteristics and placement of the nest may therefore play an important role in modulating exposure to environmental stress.

Given these constraints, nest traits that influence internal microclimatic conditions are expected to be under strong selective pressure (Heenan, 2013; Martin et al., 2017; Mainwaring et al., 2014). Nest structure and construction materials can modify internal temperature and humidity through differences in insulation, airflow, moisture retention, and exposure to external environmental conditions. Construction materials such as grasses, leaves, moss, mud, and other plant fibres differ in their thermal and physical properties and can therefore influence heat and moisture exchange within the nest (Deeming & Mainwaring, 2015). Thermal offset, defined here as the difference between internal nest temperature and ambient temperature, measures how nest conditions diverge from the surrounding thermal environment. Solar radiation, wind exposure, humidity, nest placement, and the insulation properties of different nest materials can influence

the magnitude and direction of this offset, affecting heat gain and loss within the nest (Deeming & Reynolds, 2015; Mainwaring et al., 2014). Direct solar exposure can increase internal nest temperatures above ambient conditions, producing a positive thermal offset, whereas shading can reduce radiative heat gain and limit overheating (Corimanya et al., 2024; Heenan, 2013). Wind can increase convective heat loss, particularly from exposed nests, while sheltered nest sites and surrounding vegetation can reduce airflow and moderate heat exchange (Heenan & Seymour, 2012; Mainwaring et al., 2014). Nest construction may further modify these exchanges because differences in wall thickness, material composition, porosity, and thermal conductance influence how quickly heat transfers between the nest interior and the surrounding environment (Heenan & Seymour, 2011; Lamprecht & Schmolz, 2004). Consequently, the same structural properties that promote heat retention under cooler conditions may also restrict heat dissipation under warm conditions, emphasizing that the thermal consequences of nest architecture depend on prevailing environmental conditions.

These mechanisms can differ substantially between open-cup and enclosed nest architectures. The roof and walls of an enclosed nest may provide shade, reduce direct solar heating, and limit heavy rainfall penetration. However, they entail a significant fitness trade-off, as restricted airflow in high-humidity environments can turn them into moisture traps. This reduced ventilation can promote pathogenic fungi (rot) and increase ectoparasite prevalence, as many species breed during the tropical wet season (Heenan, 2013; Deeming & Mainwaring, 2015; Price & Griffith, 2017). In contrast, open-cup nests may experience greater thermal variability and direct environmental exposure but allow greater ventilation and potentially faster drying. The consequences of these architectural differences are therefore likely to depend

strongly on prevailing environmental conditions, as well as nest materials, placement, orientation, and surrounding vegetation, rather than architecture alone. Nest architecture, as such, represents a context-dependent balance among insulation, ventilation, protection from precipitation, and exposure to solar radiation rather than a simple distinction in which one architecture consistently provides a more favourable microclimate. In a recent experimental study, Corregidor-Castro et al. (2026) demonstrated the importance of nest microclimate in the face of extreme heat, with shaded nests experiencing substantially lower nestling mortality than unshaded nests during a severe heatwave. This showed that relatively small differences in nest thermal exposure can have important consequences when environmental temperatures approach physiological limits. Thus, nest architecture reflects a balance between maintaining suitable developmental conditions and minimizing environmental stress (Medina et al., 2022; Martin et al., 2017).

Nest microclimate may further influence parental behaviour by altering the amount of incubation or brooding required to maintain suitable developmental conditions. Parents can compensate behaviourally for unfavourable nest temperatures by adjusting nest attentiveness, brooding, or shading, thereby linking the physical nest environment to parental energetic expenditure (Ar & Sidis, 2001; DuRant et al., 2019; Sheard et al., 2024). These behavioural responses may have additional ecological consequences, as changes in the frequency or duration of parental activity around the nest can affect its conspicuousness to predators (Skutch, 1985; Wang et al., 2025). The benefits associated with nest microclimate may therefore extend beyond the direct thermal environment of eggs and nestlings and interact with other selective pressures affecting reproductive success.

These interactions are particularly relevant in Grenada, where nesting birds experience a warm, humid tropical climate with substantial seasonal rainfall. Annual precipitation ranges from about 1,500 mm in the northern and southern coastal regions to about 3,800 mm in the central highlands, with the greatest rainfall generally occurring from June through November (Government of Grenada, 2014; World Bank Group, 2021). Humidity is also highest during the rainy season, approaching 80%, compared with 68-78% during the drier months (Government of Grenada, 2014). This period overlaps with the peak bird breeding season, potentially exposing active nests to the combined effects of high temperature, humidity, and rainfall. High temperatures may increase the risk of overheating, particularly when high humidity limits evaporative cooling. Repeated or heavy rainfall may saturate nest materials, increase internal humidity, and alter heat exchange within the nest. Grenada has already experienced extreme heat events, including a national maximum air temperature of 34.0°C during the record-breaking Caribbean heat season of 2020 (WMO, 2021). More recently, 2024 was the warmest year recorded across the Caribbean, consistent with the broader trajectory of increasing regional heat extremes (WMO, 2025; Coulson et al., 2025). Mean annual temperature is projected to increase by approximately 0.7-2.6°C by the 2060s (Government of Grenada, 2014), while annual precipitation may decline overall under high-emissions scenarios despite considerable uncertainty (Di Napoli et al., 2023; Government of Grenada, 2014). Understanding how these factors influence internal nest temperature and thermal offset can provide insight into whether different nesting strategies moderate or amplify environmental exposure and how their thermal consequences may change under increasingly variable climatic conditions.

2.2 Tropical vs Temperate Systems

Tropical and temperate systems differ substantially in climatic regimes, community structure, and ecological dynamics, all of which shape avian reproductive strategies. Tropical systems are characterised by relatively stable temperatures, high primary productivity, and complex, multi-layered vegetation structure (Richards, 1996). In contrast, temperate systems experience pronounced seasonal variation in temperature and resource availability, with abiotic cycles largely driving ecological processes (Whittaker, 1975).

These environmental differences are reflected in the physiology and ecology of tropical bird species. The microclimate hypothesis predicts that, because tropical understory birds evolved in a highly predictable, narrow thermal range, they lack the behavioural and physiological flexibility to cope with rapid thermal change, making them more sensitive to environmental warming (Janzen, 1967; Pollock et al., 2024). Although recent physiological studies show that many tropical birds can handle moderate temperature increases better than expected, they remain behaviourally and ecologically constrained by their specific microhabitat requirements (Monge et al., 2023). For example, while these species may possess the physiological capacity to withstand higher temperatures, their extreme specialization forces them to remain confined to cool, humid forest understories. Interestingly, Pollock et al. (2021) found that tropical birds may not be inherently vulnerable to acute heat stress, although this does not necessarily indicate equivalent tolerance to prolonged or chronic thermal exposure. Tropical birds generally exhibit narrower thermal tolerances and lower basal metabolic rates than temperate species, contributing to narrower niche breadths and greater specialization (Janzen, 1967; Londoño et al., 2015). As a result, tropical communities tend to support high species

diversity and dense ecological interactions, particularly predation. The Biotic Interaction Hypothesis predicts that stronger and more consistent species interactions in tropical systems may lead to increased predation pressure, although empirical support remains mixed (Freeman et al., 2020; Schemske et al., 2009).

Although both regions are increasingly affected by global stressors such as climate change, habitat loss, and invasive species, their impacts differ in magnitude and mechanism. In temperate systems, climate change often drives phenological shifts and mismatches between breeding timing and resource availability. In tropical systems, land-use change and habitat fragmentation remain the dominant pressures as they exacerbate microclimatic stress by stripping away canopy cover and altering local humidity. This pressure is particularly severe in island environments where limited land area restricts a species' ability to shift its geographic distribution. These differences are especially pronounced in small island systems such as Grenada, where multiple stressors may interact to influence nesting success.

2.2.1 Oceanic islands

Ecological patterns observed in continental systems often differ markedly in island environments, where isolation, limited land area, and unique evolutionary histories shape community structure (MacArthur & Wilson, 1967). Although islands occupy a small proportion of Earth's surface, they host disproportionate levels of global biodiversity and experience elevated rates of species extinction, largely driven by invasive species (Blackburn et al., 2004).

Oceanic islands typically support lower species richness but higher levels of endemism, reflecting constraints on colonization and limited habitat heterogeneity (MacArthur & Wilson, 1967). These conditions influence predator-prey dynamics and can alter selective pressures on nesting strategies. Many island bird species evolved in the absence of mammalian predators and may lack effective anti-predator defences, a phenomenon known as island syndrome (Blumstein & Daniel, 2005; Milberg & Tyrberg, 1993). This absence of historical selective pressures increases their vulnerability to novel predators following human-mediated introductions (Blackburn et al., 2004).

The introduction of invasive predators can fundamentally restructure island ecosystems through processes such as mesopredator release and the expansion of predator niches (Courchamp et al., 1999; Pearson, 2009). In systems where native predators are limited, invasive species with broad diets can exploit a wide range of prey, including nests, leading to elevated predation pressure. This can create mismatches between predator foraging strategies and the behavioural or structural defences of native birds, increasing nest vulnerability (Freeman et al., 2020). In addition, invasive predators may expand into temporal or spatial niches previously unoccupied, further increasing predation risk. Anthropogenic pressures further exacerbate these dynamics. Habitat loss and fragmentation reduce the availability of nesting habitat, while climate change increases the frequency of disturbances such as droughts and hurricanes (Mycoo et al., 2022). These stressors are particularly acute in small island systems, where limited land area restricts opportunities for population recovery and range shifts (Mycoo et al., 2022). Together, these factors create conditions in which nesting success may be strongly constrained by interacting pressures. Despite their ecological importance, tropical island systems remain

underrepresented in ecological research (de Lima et al., 2011; Lees et al., 2020). This gap is particularly evident in studies of avian reproductive success and responses to environmental stressors, which are disproportionately conducted in temperate regions (Martin, 2004). Addressing these knowledge gaps is critical for understanding population dynamics and informing conservation in systems such as Grenada, where resident landbirds experience multiple interacting pressures, including invasive predators, habitat fragmentation, and climate variability.

2.3 Tropical Bird Breeding Phenology and Life-History Strategies

Approximately 72% of bird species occupy forest habitats at tropical and subtropical latitudes (Pillay et al., 2022), making an understanding of how climate change will affect avian biodiversity in these regions essential for global conservation efforts. Breeding phenology reflects how species balance resource availability with demographic risk. In tropical systems, reproductive timing is primarily influenced by precipitation rather than temperature, with rainfall driving pulses in food availability (Hau et al., 2008; Tanaka & Tanaka, 1982). The timing and intensity of wet and dry seasons influence the abundance of fruit, flowers, and insects required for reproduction (Tobias et al., 2013). Many tropical birds initiate breeding at the transition from the dry to the early rainy season, when resource availability is highest (Hau et al., 2008; Skutch, 1985).

In response to these conditions, tropical and temperate birds exhibit contrasting life-history strategies. Tropical birds generally exhibit slower life-history strategies than temperate species, characterized by smaller clutch sizes, longer developmental periods, and reduced

parental activity at the nest, patterns often associated with minimizing detection by predators (Freeman et al., 2020; Martin, 1995; Skutch, 1949). These patterns are often linked to predation risk, as reduced parental activity at the nest may lower detectability by predators but also constrain provisioning rates, slowing offspring growth (Martin, 2004; Skutch, 1949). Longer nestling periods may allow greater physiological development, including enhanced immune function and improved post-fledging survival, but they also extend the period during which offspring remain exposed to predation and environmental conditions (Breitwisch, 1989; Greño et al., 2008; Halupka et al., 2021; Magrath, 1991; Thompson & Flux, 1991). In contrast, temperate species tend to invest in fewer, higher-intensity breeding attempts within a limited seasonal window, reflecting strong abiotic constraints on reproduction (Ricklefs, 1969; Martin, 1996). These differences highlight how environmental context shapes reproductive trade-offs and influences nesting success patterns. Consequently, suitable nest structure and microclimatic conditions may become particularly important for supporting offspring throughout these extended developmental periods (Sheard et al., 2024; Vanadzina et al., 2024)**.**

2.3.1 Phenological Patterns and Dietary Guilds in Grenada

In Grenada, breeding phenology is closely linked to seasonal rainfall patterns. The onset of rains in late May is associated with increased arthropod abundance, providing critical resources for egg production and nestling development (Tanaka & Tanaka, 1982). This relationship has been documented directly in Bananaquits on Grenada, where breeding began with the earliest rains of the wet season. However, reproductive conditions changed over the course of the breeding season: nestling mass increased and starvation declined, while nest

predation increased and fledging success decreased, suggesting a seasonal trade-off between improving food availability and increasing predation risk (Wunderle, 1982). Predation also influenced subsequent reproductive behaviour, with females sometimes abandoning both the nest site and their mate following nest predation and renesting elsewhere (Wunderle, 1984). These findings demonstrate that seasonal breeding patterns in Grenada reflect that many species initiate breeding during this period to align reproductive effort with peak resource availability.

Seasonal shifts in resource distribution also influence habitat use. During the dry season, birds may move into cooler, closed-canopy forests, while in the wet season, they often utilize lower-elevation agroforests where fruit and floral resources increase (De Ruyck, 2023). Earlier work on Bananaquits in southern Grenada similarly documented seasonal variation in space use, with adults occupying larger home ranges during the dry season than during the wet season (Wunderle, 1981). These movements reflect responses to changing environmental conditions and resource availability, which can influence both nest site selection and reproductive success.

Dietary guilds further shape breeding timing. Insectivores and frugivores typically breed earlier to match peaks in arthropod and fruit availability, whereas granivores often breed later in the season when grass seeds become more abundant (De Ruyck, 2023). These patterns indicate that reproductive timing is closely tied to resource dynamics and that successful breeding depends on aligning nesting activity with environmental conditions.

Grenadian bird communities also reflect a combination of specialization and ecological flexibility. Relatively low species richness may promote ecological release, allowing species to expand their habitat use and exploit a wider range of nesting environments (Cox & Ricklefs, 1977; Heathcote et al., 2021; Lack & Lack, 1973). However, these broader niche use patterns

may also expose nests to variable environmental conditions and predation risk. For example, open agroforests may provide high resource availability but also increase exposure to thermal stress and predators. These dynamics highlight the importance of understanding how nest structure and microhabitat interact to influence nesting success within this system.

2.4 Predator Guilds and Nest Predation Dynamics

Nest predation is a primary driver of avian reproductive success and represents one of the strongest selective pressures shaping nesting strategies (Martin, 1995). Predation dynamics are influenced by predator community composition, sensory mechanisms, and environmental context, which together determine how predators locate and exploit nests.

Nest predators can be broadly grouped into functional guilds, most commonly mammals, reptiles, and birds, each employing distinct foraging strategies. Mammalian predators typically rely on multimodal detection, integrating olfactory, auditory, and visual cues to locate nests. Reptilian predators, such as snakes common in tropical systems, use thermal and chemical cues to detect prey across multiple vegetation strata. In contrast, avian predators rely primarily on visual cues, including nest exposure and parental activity.

These differences in detection strategies influence how nest structure, placement, and parental behaviour mediate predation risk. For example, visually oriented predators may be more likely to detect exposed nests or frequent parental visits, whereas olfactory or acoustically oriented predators may exploit scent trails or nestling begging calls. As a result, predation risk is not uniform but varies depending on the interaction between predator guilds and nest characteristics.

Predation dynamics may also vary with nest density. Higher densities of active nests can increase predator search efficiency, potentially leading to density-dependent predation and influencing nesting success patterns within communities (Martin, 1988). These interactions highlight that nest predation is shaped not only by predator presence but by how predator behaviour interacts with nesting ecology.

In Caribbean systems, predator communities differ from those of mainland Neotropical regions. While snakes are dominant nest predators in many continental systems (Skutch, 1985), they are comparatively less influential in the Antilles. For example, birds comprise only a small proportion of the diet of native snakes on Hispaniola (Henderson, 1984). This suggests that historical predation pressures in island systems may have been structured differently from mainland environments.

In Grenada, native predation has historically been concentrated in arboreal and aerial strata. Key native predators include the nocturnal Grenada tree boa and the diurnal Antillean Broad-winged Hawk (see **Table 1a; Table 1b**). These predators are generalists that primarily target non-avian prey such as reptiles and small mammals, suggesting that selection pressures on nesting birds may have been relatively diffuse and spatially constrained (Campbell et al., 2022; Henderson & Pauers, 2012). As a result, lower vegetation strata may have historically represented comparatively lower-risk nesting environments.

Notably, nesting strategies in Grenadian landbirds evolved under a predator regime dominated by visually and thermally oriented predators with relatively limited specialization on avian nests.

2.4.1 Invasive Predators and Evolutionary Mismatch

Predation dynamics in island systems can shift dramatically following the introduction of invasive predators. Native predator communities exert long-standing selective pressures on species, driving the evolution of behavioural and structural responses. In contrast, invasive predators introduce novel pressures that differ in both intensity and mechanism, often resulting in an evolutionary mismatch between predator foraging strategies and prey defences.

In Grenada, invasive mammalian predators play a dominant role in shaping contemporary predation risk. Species such as the small Indian mongoose, an introduced predator established widely throughout the West Indies, have broad ecological impacts, including predation on native vertebrates and birds (Horst et al., 2001). Notably, mongooses serve as the principal wildlife reservoir of rabies on the island, with molecular evidence indicating persistent circulation of rabies virus within Grenada's mongoose population (Zieger et al., 2014). Black rats and feral or free-roaming cats likewise pose substantial threats to native fauna because they are highly adaptable generalist predators with broad diets and high reproductive potential (Bonnington et al., 2013; Trouwborst et al., 2020). Predation pressure may also vary seasonally, creating temporal overlap between predator population dynamics and avian breeding activity**.** Black rat populations, for example, show seasonal demographic patterns associated with rainfall, with juvenile and subadult recruitment contributing to higher relative abundance during the wet season in most habitats studied in Guadeloupe (Goedert et al., 2020). Similarly, Small Indian Mongooses on Grenada have an extended breeding season, with reproductive activity occurring over approximately 10 months of the year and three distinct reproductive peaks (Nellis & Everard, 1983). The principal landbird breeding period in Grenada overlaps with the wetter part

of the year, potentially increasing the temporal coincidence between heightened predator activity and vulnerable nesting stages.

These invasive predators create a continuous and multidimensional predation landscape across spatial and temporal scales. Rats exploit nests across multiple vegetation strata, often at night, whereas mongooses primarily target ground and low-vegetation nests during the day, and cats hunt ground and low- to mid-strata nests, with activity concentrated during dawn and dusk (See **Table 1a; Table 1b**). This overlap reduces the availability of safe nesting spaces and may force species into suboptimal nesting positions. In some cases, predator interactions can further intensify these effects. For example, increased predation pressure at ground and lower vegetation levels may favour shifts toward more elevated nesting sites. However, these positions may expose nests to arboreal and aerial predators, potentially redistributing rather than eliminating predation risk (Matysioková & Remeš, 2024; Remeš et al., 2012).

In addition, interactions among predator species may further alter predation dynamics. Management actions that reduce one predator species can lead to mesopredator release, where remaining predators increase in abundance or expand their ecological roles (Courchamp et al., 1999). For instance, the removal of feral cats may increase rat populations, potentially leading to greater impacts on nesting birds than the original predator assemblage (Ibáñez-Álamo et al., 2015; Ortega et al., 2021).

These dynamics highlight that predation risk in Grenada is shaped by the interactions among multiple predator guilds operating across different niches, rather than by a single dominant predator. This creates a complex and persistent predation environment that differs

substantially from historical conditions. As a result, nesting strategies that may have been adaptive under native predator regimes may no longer provide the same level of protection.

2.5 Nest Site Selection

Nest-site selection is a critical determinant of reproductive success, as it directly influences both predation risk and developmental conditions within the nest (Ricklefs, 1969; Sheard et al., 2024). Because nest construction and breeding are energetically costly, individuals must select sites that maximize offspring survival while minimizing wasted time and energy.

Birds select nesting locations that provide protection from predators, suitable microclimatic conditions, and sufficient structural support. These decisions are expressed through multiple components of nest-site selection, including nest placement within the substrate, degree of concealment, and nest height. Together, these factors determine how predators detect nests and how they experience environmental conditions.

Nest-site selection reflects an interaction between phylogenetic constraint and phenotypic plasticity. While phylogeny often determines general nest structure, behavioural flexibility allows individuals to adjust nest placement and positioning in response to local environmental conditions and predator communities (Latif et al., 2012). This flexibility may be particularly important in tropical island systems, where novel predator assemblages and environmental variability require adaptive responses.

The nest concealment hypothesis, which emphasizes physical cues, aligns closely with the Skutch hypothesis, which focuses on behavioural cues and reduced parental activity (Arslan

& Martin, 2024; Borgmann & Conway, 2015; Skutch, 1949, 1985). Together, these frameworks highlight that predation risk is shaped by both nest visibility and parental behaviour.

2.5.1 Nest Placement

Nest placement within vegetation or substrate is influenced by structural constraints, accessibility, and predator avoidance. Birds must select locations that can support the nest throughout the breeding cycle, including the weight of adults and developing offspring (Deeming & Mainwaring, 2015).

Nest structure can constrain the range of available substrates. Open-cup nests, often constructed from heavier materials, typically require stable support such as branches or forks capable of bearing weight. In contrast, enclosed nests are often lighter and constructed from flexible materials, allowing attachment to a wider range of substrates, including thin branches, vines, or suspended structures (Collias & Collias, 2014). This may enable enclosed-nesting species to exploit a broader range of microhabitats. Substrate characteristics can also influence predator accessibility. For example, nests placed on thin or flexible branches may be less accessible to heavier predators, whereas nests located on large, climbable trunks may be more vulnerable. As a result, the suitability of a nesting location depends not only on its height but also on the structural properties of the substrate.

Accessibility for parents is also an important consideration. Nest sites must allow repeated visits for construction, incubation, and provisioning, while minimizing exposure to predators. Birds may therefore select locations with suitable perches or approach routes that balance efficient access with reduced detectability.

2.5.2 Nest Concealment

The degree of nest concealment is an important determinant of reproductive success and overall fitness (Borgmann & Conway, 2015; Ibáñez-Álamo et al., 2015). Concealed nests can reduce the visual, auditory, and olfactory cues predators use to locate nests, thereby lowering predation risk (Borgmann & Conway, 2015; Remeš, 2005). However, parental activity associated with nest building, incubation, and provisioning may increase detectability, as repeated visits can attract predator attention (Arslan & Martin, 2024; Skutch, 1949). The nest concealment hypothesis proposes that birds, particularly songbirds, select nest sites within dense vegetation to reduce detectability and increase the likelihood of nest success (Borgmann & Conway, 2015). As a result, nests are often placed in sheltered microhabitats, such as bushy vegetation or areas with greater canopy cover, which may enhance camouflage (Borgmann & Conway, 2015; Deeming & Mainwaring, 2015; Latif et al., 2012; Liu et al., 2021).

The effectiveness of concealment depends on the sensory abilities and foraging strategies of the local predator community. Experimental work on Blackcaps (*Sylvia atricapilla*) demonstrated that different predator types respond to different nest-site characteristics (Remeš, 2005). Predation by visually oriented avian predators increased as concealment decreased and nest height increased, whereas predation by nocturnal rodents was largely unaffected by foliage cover and more strongly influenced by nest height. These findings highlight how predator community composition shapes the selective pressures acting on nest-site selection.

Nest concealment may also influence nest microclimate by modifying exposure to environmental stressors such as heavy rainfall, wind, and solar radiation (Deeming & Mainwaring, 2015; Scherr & Chalfoun, 2022). However, the thermal consequences of

concealment are context-dependent. In warm conditions, greater vegetation cover and shade may reduce solar heat gain and help prevent overheating, whereas in cooler conditions, greater exposure to solar radiation may provide beneficial warming (Conway & Martin, 2000; D'Alba et al., 2009). Consequently, birds may face a trade-off between selecting concealed, shaded nest sites that promote cooling and more exposed sites that permit greater solar warming (Amat & Masero, 2004; Wiebe & Martin, 1998). Dense vegetation may also restrict airflow and retain humidity, while more open sites may increase ventilation and evaporative cooling (Deeming & Mainwaring, 2015). The thermal value of nest concealment therefore depends on whether the prevailing environmental conditions require the nest to retain heat or dissipate it.

2.5.3 Nest Height

Nest height is an important component of nest-site selection because it mediates predator accessibility. The relationship between height and nesting success is often non-linear and depends on the composition of the local predator community. Nests placed higher in vegetation may experience reduced predation from ground-based predators, as accessing these locations requires greater energetic investment than foraging at lower strata. However, higher nests may become more exposed to arboreal or aerial predators, such as snakes and birds of prey (Matysioková & Remeš, 2022, 2024). Nest height therefore does not provide a universally safer nesting position. Its effect on survival depends on which predator guilds occupy different vertical strata within a particular system. With Grenada's predators occupying different vertical strata, nest height may influence which predators are able to access a nest. Lower nests may be more

vulnerable to introduced ground predators, whereas nesting higher may reduce exposure to these invasive mammals, but still leaving nests accessible to native arboreal and aerial predators.

These patterns highlight how predator community composition can shape the selective pressures acting on nest placement. For example, research on Orange-crowned Warblers on Catalina Island found that nest success increased with nest height, likely due to reduced predation from terrestrial predators in the absence of strong aerial predation pressure (Hays et al., 2022). Similarly, on many islands, invasive mammals such as black rats are major drivers of nest failure, and birds may respond by nesting higher or selecting more isolated substrates. In Hawai‘i, the endangered O‘ahu ‘Elepaio has exhibited a substantial increase in average nest height over time, likely as an adaptive response to rat predation (VanderWerf, 2012).

Nest height may also influence the microclimatic conditions experienced within nests. Nests located higher in vegetation are often more exposed to wind and temperature fluctuations, which can increase heat loss for incubating adults and developing nestlings (Deeming & Mainwaring, 2015). This suggests a potential trade-off between predator avoidance and thermal stability. Variation in nest height among species may also contribute to vertical partitioning within bird communities. Although avian assemblages have traditionally been viewed as structured primarily by competition for food resources (MacArthur, 1972; Wiens, 1989), nest predation has also been proposed as an important factor shaping community structure (Martin, 1988). By distributing nests across different vegetation layers, species may reduce competition for nesting substrates while simultaneously altering their exposure to predators. This vertical stratification can facilitate coexistence by allowing species with similar ecological requirements to occupy different nesting niches within the same habitat.

Ultimately, nest-site selection reflects a balance among multiple interacting pressures, including predator avoidance, structural constraints, energetic investment, and microclimatic conditions. The relative importance of these factors varies depending on species traits, nest architecture, and local environmental conditions.

In tropical island systems, where predator communities often include both native and invasive species, these trade-offs may be particularly pronounced. As a result, nest-site selection plays a central role in determining reproductive success by mediating both predation risk and environmental exposure. Understanding how these factors interact is essential for interpreting patterns of nesting success within this study.

2.6 Monitoring Strategies: Abundance, Productivity, and Nesting Success

Assessing avian population status relies on information such as abundance, productivity, and reproductive success. However, each of these metrics yields very different information. Abundance quantifies the number of individuals within a given area, which in turn provides a snapshot of population size and community structure (Ehrlén & Morris, 2015; Pyron, 2010). Notably, relying solely on abundance can be misleading, as high densities do not automatically indicate a self-sustaining population. In heterogeneous environments, populations can persist in sink habitats, where reproduction is insufficient to offset mortality. Long-term persistence will depend entirely on immigration from more productive 'source' habitats (Pulliam, 1988).

While productivity data, such as clutch size or fledgling output, better approximate reproductive investment, they do not entirely account for nest fate (Ricklefs & Bloom, 1977). As

a result, high productivity cannot reliably quantify successful recruitment if nests fail before fledging. In contrast, nesting success provides a direct measure of reproductive output and population viability by quantifying a successful nest as one that fledges at least one offspring. Nest predation is the primary cause of nest failure in most avian systems, and nest monitoring allows researchers to quantify predation pressure relative to other causes of failure, such as environmental stress or abandonment (Bailey et al., 2019; Ibáñez-Álamo et al., 2015; Martin, 1995). Nesting success, therefore, provides critical insight into the mechanisms driving population dynamics (Johnson, 1979).

This distinction is especially critical in island systems, where invasive predators can decouple abundance from reproductive success. In such cases, high resource availability may attract large numbers of individuals to habitats that function as abundance traps, where high densities mask underlying demographic failure. Without measuring nesting success, these habitats may be misidentified as high-quality environments, leading to misdirected conservation efforts (Johnson, 1979). Nesting success serves as an early warning indicator of population instability.

Ultimately, understanding the drivers of nesting success provides detailed demographic information needed to identify limiting life-history stages on oceanic islands. By identifying specific causes of failure, whether driven by predator guilds or microclimatic stress, researchers can develop targeted conservation strategies. However, accurate assessment depends on low-impact monitoring approaches that minimize disturbance and reduce the risk of observer-induced predation (Bailey et al., 2019; Martin & Geupel, 1993). In oceanic island systems such as Grenada, where predator communities and environmental conditions interact to influence

reproductive outcomes, monitoring nesting success is essential to assess population viability and inform conservation efforts.

Table 1a. Summary of native and invasive predators of Grenada's resident landbirds, including their biogeographic status, relative threat to landbirds, and population status and distribution in Grenada.

Species	Scientific Name	Origin	Relative Threat to Grenadian Landbirds	Population Status and Distribution in Grenada
Black Rat	*Rattus rattus*	Invasive	**High**. Known predator of eggs and nestlings and an important source of nest predation on islands.[a]	**High**. Widespread throughout all habitats.[a]
Brown Rat	*Rattus norvegicus*	Invasive	**High**. Primary driver of island nest failure. Consumes eggs and chicks.[a]	**High**. Most abundant in urban and human-modified environments.[a]
Cat	*Felis catus*	Invasive	**High**. Predates birds across multiple life stages and may also cause non-lethal behavioural responses to predation risk.[b]	**High**. Abundant and widespread throughout the island.[b]
Small Indian Mongoose	*Urva auropunctata*	Invasive	**High**. Major predator of birds and active nests, particularly in ground and lower vegetation strata.[c]	**Very high**. Approximately 6.6 mongooses/ha. Same density in all habitats. Home ranges are about 2.2-4.2 ha, but when infected with rabies, they can travel much farther. Rabid mongooses have been recorded up to 2 km from their typical habitats.[c]
Lesser Antillean Barn Owl	*Tyto furcata insularis*	Native	**Low.** Rare predator of nocturnal/roosting birds.[d]	Not well known.[d]
Antillean Broad-winged Hawk	*Buteo platypterus antillarum*	Native	**Low**. Occasional predator of fledglings.[e]	**High**. Greatest reported abundance occurs in northeastern and southwestern Grenada. Habitat use is generally consistent across seasons, although distribution may expand during the wet season as prey availability shifts.[e]
Grenada Tree Boa	*Corallus grenadensis*	Native	**Low**. Opportunistic vertebrate predator; birds represent a relatively small component of their.[f]	**High**. Island population is estimated at approximately 7,000–8,000 individuals, with density varying substantially by habitat type. The abundance of their primary prey enables them to exploit diverse environments.[f]

Note. Superscript letters identify the sources supporting information presented in each row. [a] (Duron et al., 2017; Harper & Bunbury, 2015). [b] (Medina et al., 2011; Trouwborst et al., 2020). [c] (Horst et al., 2001; Nellis & Everard, 1983; Zieger et al., 2014). [d] (Stoetzel et al., 2016). [e] (Campbell et al., 2022). [f] (Henderson & Berg, 2011; Henderson & Pauers, 2012).

Table 1b. Ecological characteristics of native and invasive predators of Grenada's resident landbirds, including biogeographic status, activity period, foraging strata, sensory cues used in prey detection, and diet.

Species	Scientific Name	Origin	Primary Activity Period	Foraging Strata	Cues	Diet
Black Rat	*Rattus rattus*	Invasive	Primarily nocturnal; may show greater diurnal activity than brown rats.[a]	Ground to canopy[a]	Olfactory; auditory; tactile	Omnivorous[a]
Brown Rat	*Rattus norvegicus*	Invasive	Primarily nocturnal[a]	Ground-level[a]	Olfactory; auditory; tactile	Omnivorous[a]
Cat	*Felis catus*	Invasive	Primarily crepuscular[b]	Ground to canopy[b]	Olfactory; auditory; tactile	Carnivorous[b]
Small Indian Mongoose	*Urva auropunctata*	Invasive	Diurnal[c]	Ground to canopy[c]	Olfactory; auditory	Carnivorous[c]
Lesser Antillean Barn Owl	*Tyto furcata insularis*	Native	Nocturnal[d]	Aerial	Visual; auditory	Carnivorous[d]
Antillean Broad-winged Hawk	*Buteo platypterus antillarum*	Native	Diurnal[e]	Aerial and upper vegetation strata; uses forest-interior and edge perches for prey detection.[e]	Visual; auditory	Carnivorous[e]
Grenada Tree Boa	*Corallus grenadensis*	Native	Nocturnal[f]	Arboreal; mid- to high-canopy[f]	Thermal; olfactory[g]	Carnivorous[f]

Note. Superscript letters identify the sources supporting information presented in each row. [a] (Harper & Bunbury, 2015). [b] (Medina et al., 2011; Trouwborst et al., 2020). [c] (Horst et al., 2001; Nellis & Everard, 1983). [d] (Stoetzel et al., 2016). [e] (Campbell et al., 2022). [f] (Henderson & Berg, 2011; Henderson & Pauers, 2012). [g] (Henderson, 2019; Henderson et al., 2009).

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Chapter 3: Methods

3.1 Study Site

This study was conducted at Belmont Estate (12°10'35.7"N, 61°37'42.6"W), located on the main island of Grenada, West Indies (Area = 344 km², Latitude: 12°03′N; Longitude: 61°45′W). Grenada's habitats include dry coastal woodlands, tropical rainforests, lush montane cloud forests, mangrove swamps, and coastal scrublands, reflecting steep environmental gradients in rainfall and elevation (Groome, 1970). Precipitation ranges from 990-1500 mm in coastal areas to 3750-5000 mm in high-montane areas, and mean daily temperatures range from 24.2°C to 26.5°C.

The island experiences a dry season from January to May and a wet season from June to December (Groome, 1970). Seasonal rainfall strongly influences resource availability, particularly arthropod abundance, which increases rapidly with the onset of rain and provides a key food resource for breeding birds (De Ruyck, 2023; Tanaka & Tanaka, 1982). Breeding activity of many terrestrial landbirds on Grenada is closely associated with the onset of the rainy season, typically beginning in late May or June and peaking between May and July (Bergen et al., 2023; De Ruyck, 2023). Although some species may breed year-round, reproductive activity generally extends from April through October (De Ruyck, 2023). Seasonal variation in rainfall and resource availability may also influence habitat use, with some species shifting between lower-elevation agroforests and higher-elevation forested habitats (De Ruyck, 2023; Williams et al., 2023).

Belmont Estate is located on the northeastern portion of Grenada in St. Patrick Parish at mid-elevation (100-215 m above sea level). The approximately 300-acre estate, formerly a plantation, now comprises a mosaic of managed, semi-natural, and regenerating habitats. The landscape is a diverse, moist agroforestry system composed of mixed plantation crops interspersed with regenerating secondary forest, gardens, and semi-open agricultural areas. Much of the estate is characterized by a shade-grown agroforestry system, where cacao grows beneath a mixed canopy of perennial crops, including nutmeg, mango, citrus, banana, and other fruit or spice trees. Managed without pesticides, this heterogeneous landscape provides a matrix of varying canopy cover, vegetation structure, and microhabitats within a regenerating secondary forest that greatly supports a wide range of avian species.

The Belmont study site was divided into two distinct habitat areas that differed in vegetation structure, land management, and levels of human disturbance, providing a useful gradient for examining how environmental variation influences nest placement, microclimate, and survival.

Site 1, referred to as the **Lower Semi-Natural Site**, serves as the main visitor area and features a semi-natural agro-garden matrix with cultivated crops, ornamental plantings, and landscaped gardens. This area represents a human-modified edge habitat, and vegetation is dominated by ornamental shrubs (e.g., Bougainvillea), royal and king palms, scattered perennial crops, and roadside vegetation such as shrubs and cacti. Regular grounds maintenance, including clearing fallen plant debris and trimming vegetation, results in a relatively open understory and high levels of human activity. A nearby stream corridor of secondary forest was excluded from the study due to accessibility and safety constraints.

Site 2, designated the **Upper Agroforest Site**, is located at a slightly higher elevation and serves as the primary production area. It consists of a mosaic of areas, including mixed-fruit and spice agroforest patches and more open areas with row crops such as pigeon pea and other vegetables. The Upper Agroforest Site is characterized as a stratified agroforestry system with greater canopy cover and vegetation density, interspersed with dense patches of regenerating secondary forest, scrub, and lianas. Edge pathways and trails were present throughout the area, which contributed to habitat connectivity and canopy complexity. Data collection was limited on the steeper slopes because of logistical and safety concerns related to unstable terrain later in the season. Ground-level nutrient cycling is maintained by leaving harvested cocoa pods to decompose, contributing to a more complex microhabitat for ground-level predators. Human disturbance is minimal at this site as tourist access is restricted. However, residential houses are present along the trail.

3.2 Field Methods

Research was conducted from April 29 to July 21, 2023, and from May 8 to May 27, 2025. Fieldwork periods were selected to coincide with the peak nesting activity, maximizing nest detection and ensuring a robust sample size, while acknowledging that many Grenadian species breed year-round or have extended breeding seasons (Bergen et al., 2023; De Ruyck, 2023).

3.2.1 Study Species

Grenada has 35 resident landbird species, many of which are subspecies with restricted ranges (Rivera-Milán et al., 2015; Rusk, 2003). This study focused on the most common nesting species in the area (De Ruyck, 2023; Devenish-Nelson & Nelson, 2021; Williams et al., 2023), leading to the inclusion of 11 focal species representing a range of nesting strategies, habitat associations, and foraging guilds. This included 4 enclosed nesters: Bananaquit, Lesser Antillean Bullfinch, Grenada Wren, and Black-faced Grassquit, and 7 open-cup nesters: Spectacled Thrush, Lesser Antillean Tanager, Gray Kingbird, Tropical Mockingbird, Yellow-bellied Elaenia, Common Ground Dove, and Eared Dove.

Data collected in 2023 focused on the nesting success of native landbirds and served as the primary dataset for this study, encompassing all focal species. The second, shorter field season in 2025 examined microclimate differences between the two dominant nest types (open and enclosed) identified in 2023. Data collection in the second field season was restricted to Lower Semi-Natural Site to maximize sampling efficiency and included a subset of species, comprising three open-cup nesters and two enclosed-nesters. Although nesting success was not an objective of this field season, all active nests (n = 36) were monitored until the end of the breeding attempt or the conclusion of the field season to document breeding behaviours of these species and to record any potential nest depredation events as supplementary observations to the 2023 field season.

3.3 Data Collection

3.3.1 Nest Detection, Monitoring, and Fate Assessment

The following protocol was followed for both the 2023 and 2025 field seasons. Nests were located using a combination of systematic searches, behavioural cues from adult birds, and opportunistic observations in order to maximize detection probability and minimize the bias associated with cryptic nest placement (Bailey et al., 2019; Martin & Geupel, 1993; Rodewald, 2014). To ensure thorough, consistent coverage and facilitate organized, repeatable surveys, each site was divided into smaller subsections, where observers searched for nests by traversing the length of each area in a series of straight paths approximately 1 m apart. Navigation was aided by the GPS and compass functions within the ArcGIS Field Maps mobile application. These subdivisions were used solely to organize search effort.

Avian behavioural cues were used to locate nests by observing and following individuals displaying behaviours associated with reproduction or parental care. Indicators of active nests included carrying nesting material, repeatedly transporting food to one site multiple times a day, persistent alarm calling, territorial defences like mobbing or mate guarding, and repeated movements to and from a discrete location. Courtship behaviours such as singing and food offering, alongside heightened adult vigilance and repeated inspection of a particular area, were also used as indicators of nearby nesting activity (Bailey et al., 2019; Martin & Geupel, 1993).

Once a potential active nest was located, the GPS location was marked using ArcGIS Field Maps. Photographs were taken from multiple angles, including the nest, supporting substrate, and surrounding habitat. Notes on nest characteristics, nesting substrate, surrounding

vegetation structure, microhabitat characteristics, and species identity were recorded to aid in relocating the nest for subsequent monitoring and nest checks.

To determine fledging dates as accurately as possible, nests and contents were monitored and examined at 2-4 day intervals (Martin & Geupel, 1993; Winter et al., 2003). Each monitoring session began with a 15-minute observation period to assess nest activity and parental behaviour from a discrete location prior to approaching the nest. This was followed by approaching the nest to check its contents using an endoscope. If adults were still present in the nest, they were gently flushed prior to inserting the endoscope. Time spent at each nest was limited to 10 minutes to minimize disturbance. Species identity was confirmed during this stage if it had not been previously identified.

Nest searches and subsequent monitoring sessions and nest checks were conducted during the morning hours, shortly after sunrise until the afternoon (05:30-13:00), when breeding-related activity such as nest building and offspring provisioning was at its highest. Monitoring schedules were adjusted to ensure that nests visited later in the day were also checked earlier during subsequent visits, minimizing temporal bias in the detection of nest activity. To further reduce observer or confirmation bias, monitoring duties were alternated between observers, ensuring that no individual monitored the same nest in consecutive sessions. For safety reasons, field observations were cancelled during tropical storms, persistent lightning and thunder, and continuous heavy rainfall.

A nest was considered successful if at least one offspring fledged (Bailey et al., 2019; Martin & Geupel, 1993). When nest fate was unclear, 15-minute fledge checks were conducted on empty nests suspected of having fledged (i.e., nests with nestlings 8 days or older when the

nest was found empty). During these checks, the immediate area was surveyed for fledglings that may have left the nest, and adult behaviour was observed for evidence of fledgling provisioning or signs of agitation (Bailey et al., 2019; Martin & Geupel, 1993).

Data recorded for each nest included clutch size, nest stage, presence of brood parasites, and any other notable behaviour or nest content notes (e.g., unhatched eggs, insects, or parasites in the nest). Nests were monitored at least twice before classifying them as inactive to ensure confidence in distinguishing successful from failed nests.

In 2023, monitoring continued until all focal breeding attempts concluded. To avoid logistical constraints and ensure all selected nests could be effectively monitored, a cut-off date of July 1, 2023, was established, after which nest searching concluded and no new nests were included in the study. In 2025, monitoring continued until focal breeding attempts concluded. No cut-off date was established for this season due to its length, and maximizing the number of nests found was necessary.

During all field activities, human observers remained vigilant to potential nest predators and minimized the risk of attracting attention to active nests (Bailey et al., 2019; Martin & Geupel, 1993). This minimally-invasive, non-destructive approach was effective for locating nests and potential nest sites, and nests and their contents were not touched during these activities. All research procedures followed the University of Manitoba Animal Care Committee guidelines.

3.3.2 Nest Cameras

Motion-sensor trail cameras were deployed during the 2023 field season as a supplementary method to assess nesting success. Cameras were installed to identify predator species visiting nests, capture predation events, and determine whether predators were native or invasive. Cameras also aided in identifying breeding species for nests that could not be visually confirmed during field monitoring and provided additional observations of nesting behaviour.

Trail cameras were positioned at least 50 cm away from nests once a minimum of one egg was observed. When vegetation allowed multiple placement options, the farthest position from the nest while maintaining adequate image quality was selected to minimize disturbance and reduce the likelihood of nest desertion. Once motion was detected, cameras captured a burst of three photos. In low-light conditions, a filtered red flash was used to illuminate the scene while minimizing disturbance and reducing the likelihood of attracting predators to nest sites. If a camera could not be placed directly at a nest due to nest height, dense vegetation, or other logistical constraints, it was positioned to monitor the ground area surrounding the nest substrate. This setup enabled the detection of predators approaching the nest site that could pose a threat. As ten trail cameras were available for this study, this method was used when equipment could be allocated.

Cameras remained in place until the breeding attempt concluded, and batteries and SD cards were replaced between nests. Camera deployment was recorded in ArcGIS Field Maps. Due to the small size and rapid movements of many bird species, images were often of low quality or failed to capture clear activity at the nest. Adobe Lightroom was used to enhance images and improve clarity for identification and analysis.

3.3.3 Nest Microclimate Assessment

Nest microclimate assessments were conducted during the 2025 field season to build on 2023 findings by examining differences in internal and external nest temperatures between open and enclosed nest types. Both active and inactive nests were sampled to evaluate variation in nest microclimate and determine whether thermal offset differed between occupied and empty nests. Temperature was recorded using Thermochron iButton data loggers (DS1921G-F5#; 5.89 mm height × 17.35 mm diameter) with one sensor embedded vertically within the nest wall and a second sensor attached to nearby vegetation directly outside the nest to record ambient temperature. External sensors were positioned in shaded locations facing the nest to minimize the influence of direct solar radiation on temperature measurements. Sensors were installed using tweezers to ensure precise placement and concealment within the nest structure. Deployment was delayed until at least two eggs were present to reduce disturbance and ensure a substantial reproductive investment had been made, so as to reduce the risk of nest abandonment.

Prior to deployment, nests were observed for 15 minutes to assess activity and confirm species identity. Nest contents were then inspected using an endoscope camera to verify stage and determine optimal sensor placement to minimize disturbance. Prior to deploying iButton data loggers in inactive nests, two monitoring sessions were conducted to confirm inactivity and ensure nests were not in the building or laying stage. For nests higher than 1.5 m, a ladder was used to facilitate accurate placement and reduce disturbance. However, nests higher than 5 m could not be reached and thus were inaccessible and excluded from sampling. Additionally, inactive nests that were not structurally sound were also excluded because the lack of adult maintenance led to rapid deterioration, an issue which was exacerbated by the onset of seasonal

rainfall during the study period. This was especially true in enclosed nests, where weakened nest walls could no longer securely retain an embedded sensor without compromising the nest's structural integrity.

Each iButton recorded temperature at five-minute intervals over a 24-hour period, with a delayed start to synchronize logging across nests and between internal and external sensors. Monitoring points and subsequent iButton deployments were recorded in ArcGIS Field Maps, including the date and time of installation, retrieval time, sensor serial number, placement location, and relevant field observations. To prevent contamination, observers washed their hands with mild, unscented soap after handling each nest and sanitized all equipment with unscented wipes between uses.

Due to the shorter field season, the 2025 sample size was substantially smaller than in the 2023 field season and included fewer species. This protocol was designed to minimize the number of animals involved while still obtaining statistically meaningful results by maximizing data collection within the limited timeframe. Nest contents were handled only when absolutely necessary to ensure that iButtons could be securely positioned in the nest wall with minimal disturbance to its integrity and contents. Since sensors were placed once at least two eggs were present, occasional incidental contact with eggs or nestlings occurred and was avoided unless absolutely necessary. In particularly restricted situations, contents were gently shifted to the side to enable swift and, secure placement of the sensor. Time spent at each nest was limited to approximately 10 minutes during initial iButton embedding and 5 minutes during each subsequent check. All research procedures were conducted in accordance with the guidelines of the University of Manitoba Animal Care Committee.

3.3.4 Nest-site Microhabitat Survey

All measurements were conducted, when possible, following the completion of the breeding attempt. This procedure was carried out during both the 2023 and 2025 field seasons. Four different surveys were conducted:

1. **Nest height**: Nest height was initially estimated at nest discovery and later measured with a rangefinder after the breeding attempt was completed to maximize accuracy and minimize disturbance. Direct measurements with a tape were taken when nests were accessible and low enough to reach. In cases where nests failed before accurate measurements could be obtained, but their position was still clearly evident, vegetation surveys were still conducted with notes documenting the event. However, if the original nest location was not identifiable, initial estimates were retained. Measurements were recorded in meters.
2. **Nest substrate:** Nest type (open-cup or enclosed) and type of substrate the nest was built on (shrub, vine, tree, palm, or anthropogenic structure) were recorded.
3. **Substrate height**: Defined as the height of the supporting vegetation or substrate in which a nest was built, measured from the ground to its highest point. This metric provides context for nest placement within the vegetation structure and was measured using the same protocol as nest height. Used to derive additional nest-placement metrics, including relative height (nest height divided by substrate height) and distance to top (substrate height minus nest height), which were incorporated into subsequent statistical analyses.

4. **Canopy density:** Measured to quantify the overhead cover surrounding each nest. A 25-cell grid mirror was used to obtain readings at three points along a linear transect, beginning directly beneath the nest and extending outward at 2 m intervals. The transect direction was randomly selected. At each point, the proportion of grid cells reflecting canopy cover was calculated (n/25), and the mean of the three readings was used as the final estimate of canopy density, expressed as a percentage.

3.3.5 Statistical Analyses

3.3.5.1 Nesting Success Data

To evaluate how nest structure, microhabitat characteristics, and seasonal timing influenced nesting success, data from the 2023 field season were analyzed in R using the logistic exposure method (Shaffer, 2004). This approach was implemented within a generalized linear model (GLM) framework with a binary response variable representing survival or failure during each observation interval. Logistic exposure models were fit using a binomial error distribution and a modified logit-link function that accounted for variation in exposure periods (i.e., the number of days between nest visits), allowing unequal-duration monitoring intervals to be included in the analysis. This allowed nests discovered at different stages of the breeding cycle to be incorporated and to contribute information over the periods for which they were observed. Nests with an unknown final fate could also contribute survival information up to their final active monitoring interval, thereby retaining available observations without assuming their subsequent fate. This approach maximized the use of available data, making it particularly useful for studies with limited nest data. Unlike traditional approaches such as the Mayfield method,

logistic exposure does not require assumptions about the timing of nest failure within an observation interval and allows daily survival to be modelled as a function of both continuous and categorical explanatory variables (Shaffer, 2004).

Fixed effects for clutch size and tree diameter (cm) were not included in the candidate models because of extensive missing data. Preliminary analyses further indicated that these variables did not improve model fit or predictive performance. Additionally, alternative measures of nest placement, including relative height and distance to the canopy top, were evaluated in separate candidate models but were not retained in the top-supported models ($\Delta AIC_c < 2$), indicating that absolute nest height provided the most parsimonious representation of vertical nest placement.

Due to the limited sample size, daily survival rate was not modelled separately by species. Incorporating species as a random effect may have resulted in unreliable variance estimates and potential over-parameterization of the models. Analyses were conducted across all nests to assess the effects of microhabitat characteristics on nesting success, while explicitly accounting for differences between open and enclosed nest types.

Site was included as a fixed effect to account for differences in habitat structure and nesting phenology between the two study areas. Exploratory analyses indicated that distributions of nest height, canopy density, Julian date, and nest type differed between sites. Because only two sites were included, site was not modelled as a random effect. Inclusion of Site improved model support ($\Delta AIC_c < 2$) and was therefore retained as an additive fixed effect to control for site-level variation. Nest fate over each monitoring interval (0 = failed, 1 = survived) was used as the binary response variable, and the fixed effects of nest type and site were included as

categorical predictors in all candidate models. Pairwise correlations among continuous predictors were examined prior to model fitting to assess collinearity.

Candidate models were specified *a priori* and included fixed effects for nest type (open, enclosed), Site (Lower Semi-Natural Site, Upper Agroforest Site), nest height (m), Julian date, and canopy density (%). Interaction terms between nest type and the continuous predictors were included to test whether the effects of microhabitat characteristics and seasonal timing on nesting success differed between nest types. Continuous predictors were standardized (mean = 0, SD = 1) to improve coefficient comparability, reduce scaling-related differences among predictors, and allow direct comparison of effect sizes (Muff et al., 2016).

Models were built additively based on their ability to assess ecological predictive power (**Table 2**). Variance inflation factors (VIFs) were calculated to assess multicollinearity among predictors in candidate models. Over-dispersion and model goodness-of-fit were evaluated by dividing the residual deviance by the residual degrees of freedom and using the Hosmer-Lemeshow test, respectively. Models that met these diagnostic criteria were retained and compared with a null model assuming constant survival, single-predictor models to evaluate the independent effect of each variable, and with the null model (which represented the hypothesis that daily survival remained constant across all observations), serving as a baseline for model comparison.

Model selection was conducted using Akaike's Information Criterion corrected for small sample sizes (AIC_c), and models were ranked by AIC_c, with the top-supported model defined as the one with the lowest AIC_c and the highest model weight (w_i). In the case of multiple competitive candidate models ($\Delta AIC_c < 2$), model averaging was performed to account for

model selection uncertainty and reduce the risk of overfitting (Burnham & Anderson, 2002; Shaffer, 2004). Both full and conditional model averages were calculated. The full average incorporated all candidate models, shrinking coefficients of unsupported variables toward zero and providing a conservative estimate of variable importance. The conditional average included only models in which a given predictor was present, reflecting its effect size when included (Shaffer, 2004). Model-averaged coefficients from the full average were exponentiated to obtain odds ratios to quantify each predictor's influence on daily survival. For predictors involved in interaction terms, effects were interpreted within the context of the interaction structure rather than as marginal main effects. 85% confidence intervals were used here in accordance with information-theoretic practice (Arnold, 2010).

For interpretation and visualization, top-supported models ($\Delta AIC_c < 2$) were refit using unstandardized predictors to allow estimates to be expressed on original measurement scales. Predicted daily survival rates (DSR) were generated under specific conditions by holding non-focal variables constant (typically at their mean values and at the reference site). Predicted values were generated using model-averaged coefficients, and uncertainty was quantified using standard errors to calculate confidence intervals (95%) on the logit scale, which were then back-transformed to probabilities. Finally, cumulative survival rate (CSR) was calculated by raising daily survival probability to the power of 29, representing the average nesting period across focal species. This allowed daily survival estimates to be translated into biologically meaningful measures of overall nesting success.

3.3.5.2 Nest Microclimate Data

To examine how nest structure, nest stage, and microhabitat characteristics influence nest microclimate, iButton temperature data collected during the 2025 field season were analyzed in R. Nest microclimate was evaluated as the temperature difference (ΔT) between internal nest temperature (T_i) and ambient temperature (T_a). This metric represents the thermal offset ($\Delta T = T_i - T_a$) of the nest interior relative to its immediate surrounding environment. Positive ΔT values indicated that internal nest temperatures were warmer than ambient conditions, whereas negative values indicated that the nest interior was cooler than the surrounding environment. To account for potential diurnal variation in internal nest microclimate, we evaluated changes in thermal offset (ΔT) over the full 24-hour cycle rather than relying solely on an overall mean difference**.** Generalized additive mixed models and generalized least-squares models were used as complementary analytical approaches. Generalized additive mixed models were used to characterize nonlinear diurnal temperature patterns as a function of time of day, nest type, and nest stage, with time modelled as a cyclic predictor and within-nest temporal dependence explicitly represented using a residual correlation structure. Generalized least-squares models, in turn, quantified average differences in thermal offset among nest types and stages while accounting for repeated observations within nests and temporal autocorrelation.

Fixed effects considered across Generalized additive mixed models and generalized least-squares model analyses included nest type (open or enclosed) and nest stage (empty, incubation, or nestling). Nest identification number (NID) distinguished repeated observations within individual nests and defined within-nest temporal correlation and cluster structure. Final analyses

were restricted to nests with paired internal and external temperature measurements from iButton data loggers.

i. *Generalized Additive Mixed Model Analysis*

Generalized additive mixed models were used to examine nonlinear diurnal patterns in internal nest temperature and thermal offset and to determine whether the shape of the diurnal internal-temperature pattern differed between nest types while accounting for nest stage. Generalized additive mixed models allow nonlinear relationships to be represented using smooth functions of covariates while accommodating correlation among repeated observations (Wood, 2017). The degree of smoothness is estimated from the data, allowing complex temporal patterns to be modelled while limiting overfitting.

Models were fitted with a Gaussian error distribution and identity link. Hour of day was modelled using a cyclic cubic regression spline (bs= “cc”; $k = 10$) to represent the repeating 24-hour temperature cycle. Cyclic boundary knots were specified at 0 and 24 h so that fitted temporal functions joined continuously across the 24-hour boundary. An elapsed-time index was calculated separately for each nest as the number of 5-minute intervals since the beginning of its recording period. This ensured that temporal correlation was modelled independently within each unique nest. Timestamp spacing, duplicate time values, and gaps in recording sequences were examined prior to model fitting.

Models containing continuous autoregressive [CAR(1)] and autoregressive moving-average [ARMA(1,1)] correlation structures were compared while holding the fixed-effect and

smooth structures constant. Models assuming homogeneous residual variance were also compared with models allowing residual variance to differ among nest stages using a variance-identity (varIdent) structure. Model support was evaluated using Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), and autocorrelation functions of normalized residuals. These comparisons supported an ARMA(1,1) temporal correlation structure within nests together with stage-specific residual variance, and this covariance structure was retained in subsequent models. An additional random intercept for nest identity was evaluated while retaining identical fixed effects, smooth terms, correlation structures, and residual variance structures. The nest-level random intercept did not improve model fit and was therefore not retained in the final generalized additive mixed models. Final models incorporating the selected ARMA(1,1) correlation structure and stage-specific residual variance were fitted using restricted maximum likelihood (REML).

Three generalized additive mixed models were used to evaluate diurnal thermal dynamics (**Table 3**). Model one, thermal-offset, assessed whether thermal offset exhibited a nonlinear pattern across the 24-hour cycle. Thermal offset was modelled as a function of nest type, nest stage, their interaction, and a common cyclic smooth term of hour (s(hour)). Model two, internal-temperature, examined inner nest temperature while accounting for ambient temperature to determine whether internal nest temperature exhibited a nonlinear diurnal pattern across nests after accounting for variation associated with ambient temperature, nest type, and stage. Internal nest temperature was modelled as a function of ambient temperature, nest type, nest stage, their interaction, and a common cyclic smooth of hour (s(hour)). The third nest-type-specific diurnal-pattern model tested whether the shape of the diurnal internal-temperature trajectory differed

between open-cup and enclosed nests. This model extended the second generalized additive mixed model by adding a difference smooth for open-cup nests (s(hour, by=type_smooth)). An ordered-factor difference-smooth parameterization was used, such that the common cyclic smooth represented the reference diurnal pattern and the additional smooth represented the deviation of open nests from that pattern. We evaluated evidence for nest-type-specific diurnal trajectories primarily from the estimated type-specific difference smooth term and its associated significance test, using AIC and BIC as supplementary measures of whether including the difference smooth term improved overall model fit.

Model predictions were generated for the full 24-hour cycle for each nest-type and nest-stage combination. For the thermal-offset model, predicted ΔT and associated 95% confidence intervals were derived directly from the fitted generalized additive mixed model. For the internal-temperature model, ambient temperature was held constant at its observed overall mean, so that the predicted curves captured variation in internal nest temperature over the day after accounting for ambient conditions.

Model diagnostics were assessed using normalized residuals from the underlying *lme* component of each generalized additive mixed model. Residual autocorrelation was examined using autocorrelation functions of normalized residuals. The adequacy of the cyclic spline basis dimension was assessed using gam.check(), and models fitted with a larger basis dimension (k = 15) were examined as a sensitivity analysis. Concurvity was also examined, particularly for models containing both ambient temperature and hour of day, to assess whether shared temporal structure among predictors compromised estimation. Residual-versus-fitted and normal Q–Q plots were examined to assess residual patterns and normality, respectively. Parametric effects of

nest type, nest stage, and their interaction within the generalized additive mixed models were included to account for differences in overall thermal conditions among groups while evaluating diurnal thermal patterns. Formal inference regarding mean differences in thermal offset among nest types and stages was conducted separately using the generalized least-squares analysis with nest-level cluster-robust inference.

ii. *Generalized Least-Squares Analysis*

Generalized least-squares models were used to evaluate how nest structure, nest stage, microhabitat characteristics, and clutch size influenced thermal offset (ΔT). This approach allowed temporal dependence and heterogeneous residual variance among repeated temperature observations to be represented explicitly through the within-nest correlation and variance structures. Prior to the construction of the candidate fixed-effect models, alternative ARMA structures were compared using AIC, BIC, and normalized residual autocorrelation. ARMA(1,2) was retained because it provided strong model support, adequately accounted for residual autocorrelation, and could be estimated consistently across the candidate model set. A nest-level random intercept was evaluated but did not improve model support after accounting for temporal autocorrelation and was therefore not retained. Models allowing residual variance to differ among nest stages were also compared with models assuming homogeneous variance, and stage-specific residual variance was retained based on AIC and likelihood-ratio tests.

Following selection of the covariance structure, candidate fixed-effect models were constructed *a priori* to evaluate the relative influence of nest type, nest stage, canopy density (%), nest height (m), and clutch size on thermal offset. Predictors were added progressively to

assess the predictive value of hypothesized ecological relationships. The resulting candidate set of models included a null (constant) model, single-predictor models for each explanatory variable, and an additive model containing nest type and nest stage. A nest type and nest stage interaction model was then used to evaluate whether differences in thermal offset between nest types varied among nesting stages. Canopy density, nest height, and clutch size were subsequently added individually and in biologically relevant combinations to determine whether these additional variables improved model support beyond the nest type and nest stage interaction (**Table 4**).

Model selection was done by ranking candidate models by AIC, with the top-supported model defined as the one with the lowest AIC and the highest model weight (w_i). Models with $\Delta AIC < 2$ were considered competitive and in the case of multiple competitive candidate models ($\Delta AIC < 2$), the most parsimonious, biologically interpretable model from the top-ranked set was selected for inference. All candidate models used the same ARMA(1,2) temporal correlation structure and stage-specific residual variance structure and were fitted using maximum likelihood (ML) so that models differing in their fixed effects could be compared directly.

The selected generalized least-squares model was refitted using restricted maximum likelihood (REML) for final parameter estimation. Inferential tests were based on CR2 cluster-robust variance estimates calculated at the nest level, with Satterthwaite small-sample degrees-of-freedom corrections to account for the small number of independent nests relative to the large number of repeated observations. The overall nest type and nest stage interaction was assessed using a small-sample cluster-robust Wald test with an approximate Hotelling's T^2 correction.

Model-estimated means and CR2-based 95% confidence intervals were calculated for each nest type and nest stage interaction combination. Contrasts between open and enclosed nests were evaluated separately within each nest stage using CR2 cluster-robust variance estimates and Satterthwaite degrees of freedom. Holm adjustment was applied to *P*-values across the three stage-specific comparisons, and results were visualized using model-estimated means and their CR2-based 95% confidence intervals.

Table 2. *A priori* candidate models used in the logistic-exposure analysis of daily nest survival during the 2023 field season. Candidate predictors included nest type (open, enclosed), Site (Upper Agroforest Site, Lower Semi-Natural Site), nest height (m), canopy density (%), and Julian date (days since 1 April 2023), together with biologically relevant interactions. The null model represents constant daily nest survival across observations. Continuous predictors were standardized (mean = 0, SD = 1) to allow comparison of model coefficients.

Model Class	Model Structure
Constant	Null
Single-predictor	Nest Type Site Nest Height Canopy Density Julian Date
Additive	Nest Type + Site Nest Type + Site + Nest Height Nest Type + Site + Canopy Density Nest Type + Site + Julian Date Nest Type + Site + Nest Height + Canopy Density Nest Type + Site + Canopy Density + Julian Date Nest Type + Site + Nest Height + Canopy Density + Julian Date
Interaction	(Nest Type x Nest Height) + Site (Nest Type x Canopy Density) + Site (Nest Type x Julian Date) + Site (Nest Type x Nest Height) + Site + Julian Date (Nest Type x Canopy Density) + Site + Julian Date (Nest Type x Nest Height) + (Nest Type x Canopy Density) + Site (Nest Type x Nest Height) + (Nest Type x Julian Date) + Site

Table 3. Structure of generalized additive mixed models used to evaluate diurnal nest microclimate during the 2025 field season. Response variables included thermal offset ($\Delta T = T_i - T_a$; °C) and internal nest temperature (T_i; °C). Models included nest type (open, enclosed), nest stage (empty, incubation, nestling), their interaction, ambient temperature (T_a; °C) and a cyclic smooth term of hour of day (s(hour)). The type-specific internal-temperature test model additionally included a difference smooth term (s(hour, by= type_smooth)).

Model Name	Response Variable	Model Structure
Thermal offset	ΔT	Nest Type x Nest Stage + s(hour)
Internal temperature	T_i	T_a + Nest Type x Nest Stage + s(hour)
Nest-Type-specific diurnal pattern	T_i	T_a + Nest Type x Nest Stage + s(hour) + s(hour: Open)

Table 4. *A priori* candidate generalized least-squares models used to evaluate variation in nest thermal offset ($\Delta T = T_i - T_a$; °C) from the 2025 iButton temperature data. Candidate models included nest type (open, enclosed), nest stage (empty, incubation, nestling), canopy density (%), nest height (m), and clutch size as biologically relevant predictors.

Model Class	Model Structure
Constant	Null
Single-Predictor	Nest Type
	Nest Stage
	Nest Height
	Canopy Density
	Clutch Size
Additive	Nest Type + Nest Stage
Interaction	(Nest Type x Nest Stage)
	(Nest Type x Nest Stage) + Canopy Density
	(Nest Type x Nest Stage) + Nest Height
	(Nest Type x Nest Stage) + Clutch Size
	(Nest Type x Nest Stage) + Canopy Density + Nest Height
	(Nest Type x Nest Stage) + Canopy Density + Clutch Size
	(Nest Type x Nest Stage) + Nest Height + Clutch Size
	(Nest Type x Nest Stage) + Nest Height + Canopy Density + Clutch Size

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Chapter 4: Results

4.1 Nesting Success Data (2023)

During the 90-day period (April 29 to July 21, 2023) of the 2023 field season, 290 nests were found, of which 107 were active. Of the 107 active nests, 27 were excluded because they were found after the July 1 cutoff date, leaving 80 monitored nests. Additionally, 10 nests were removed due to unreliable data or safety constraints that limited monitoring. This resulted in 70 nests across 11 species included in the final analysis. Overall, 56% of nests successfully fledged offspring, while 36% failed (**Table 5**). The remaining 8% had unknown outcomes due to incomplete breeding cycles at the end of the field season.

4.1.1 Logistic Exposure Analysis

Model selection indicated that three candidate models ($\Delta AIC_c < 2$; **Table 6**) provided strong support for predicting nesting success data and were considered competitive. All competitive models included site as a fixed categorical effect and an interaction between nest type and nest height. The most parsimonious model included no additional covariates and had the highest Akaike weight ($\Delta AIC_c = 0.00$, $w_i = 0.338$). The next two candidate models included an additional interaction between nest type and canopy density ($\Delta AIC_c = 1.40$, $w_i = 0.167$) and an additive effect of Julian date ($\Delta AIC_c = 1.70$, $w_i = 0.144$), respectively.

Model-averaged estimates are reported from the full-average and relative to the reference categories of enclosed nests and Upper Agroforest Site. Parameter estimates indicated higher daily survival probabilities for open-cup nests when holding Site constant at the reference level Upper Agroforest Site, and holding nest height, canopy density, and Julian date at their mean

values (β = 1.0031 ± 0.647; **Table 7; Figure 1**). Model-averaged predictions indicated that open-cup nests had a daily survival rate of 98.7% (95% CI: [0.962, 0.996]; **Table 8**) with a corresponding cumulative survival probability of 69.1% (95% CI: [0.326, 0.886]), whereas enclosed nests had a DSR of 96.6% (95% CI: [0.933, 0.983]), with a corresponding CSR of 36.9% (95% CI: [0.132, 0.615]). Overall, open-cup nests had approximately 2.7 times the odds of daily survival (OR = 2.73; 85% CI: [1.08, 6.91]; **Table 7**). The interaction between nest height and nest type showed a strongly supported positive association (β = 2.0476 ± 1.0309), indicating that the effect of nest height on daily survival differed between open and enclosed nest types. In particular, this interaction indicates that the effect of nest height on daily survival was substantially greater for open-cup nests than for enclosed nests (OR = 7.75; 85% CI: [1.76, 34.12]). Enclosed nests, in contrast, showed little change in daily survival across observed nest heights (β = 0.152 ± 0.448; **Figure 2**). The interaction between nest type and canopy density was also supported (OR = 0.44; 85% CI: [0.21, 0.94]), though it was weaker (β = -0.210 ± 0.443) and carried less weight (w_i = 0.26) than the nest height interaction. This relationship indicates that increasing canopy density was associated with reduced daily survival in open-cup nests, whereas the effect was weaker or absent in enclosed nests (β = 0.0154 ± 0.120; **Figure 3**). Site had a positive relationship with survival (β = 0.856 ± 0.468), where nests built at the Lower Semi-Natural Site had approximately two times higher odds of survival (85% CI: [1.20, 4.61]) compared to nests built at the Upper Agroforest Site. Julian date did not substantially improve model fit and showed limited support as a predictor of survival (**Table 7**).

To evaluate whether the inclusion of Columbidae species (n = 4) influenced model outcomes, analyses were repeated with these nests removed. Model selection results, model-averaged coefficients, and the direction of ecological effects were unchanged, indicating that the main patterns were robust and not driven by the inclusion of Columbidae.

4.2 Nest Microclimate Data (2025)

During the 30-day period (May 5 to May 27, 2025) of the 2025 field season, a total of 51 nests were located. Of these nests, 35 were excluded due to accessibility constraints, primarily their height, and because they were unsuitable inactive nests. Overall, iButtons were deployed to 16 nests. However, three of these nests were subsequently excluded from the final analysis due to the loss of one or more iButtons, resulting in a final sample size of 13 nests for analysis (**Table 9)**.

4.2.1 Generalized Additive Mixed Model Analysis

Generalized additive mixed models were used to characterize nonlinear diurnal patterns in thermal offset and internal nest temperature. The presence and strength of these temporal patterns differed across the response variables. Diagnostic checks provided no evidence that the cyclic spline basis dimension was inadequate for the two primary generalized additive mixed models. For the thermal-offset and internal-temperature models, the *k*-indices were 0.98 (P = 0.23) and 0.95 (P = 0.14), respectively. Covariance-structure comparisons supported the use of an ARMA(1,1) temporal correlation structure with stage-specific residual variance for all generalized additive mixed models. An additional random intercept for nest identity did not

improve model support and was therefore excluded from the final generalized additive mixed models.

The thermal offset model found no evidence of a nonlinear diurnal pattern in thermal offset after accounting for nest type, nest stage, temporal autocorrelation, and stage-specific residual variance. The cyclic smooth term for hour was reduced to zero complexity and was not statistically significant (*s*(hour): edf < 0.001, $F < 0.001$, $P = 0.688$; **Table 10; Figure 4)**. The model had an adjusted R^2 of 0.368. Consequently, predictions showed little change in thermal offset across the 24-hour period within each nest type and nest stage. Differences in the vertical position of the predicted curves across nest type and nest stage combinations reflected the model's parametric component rather than temporal changes in thermal offset.

In contrast, the internal-temperature model showed a strong nonlinear diurnal pattern in internal nest temperature across nests, after accounting for simultaneous ambient temperature, nest type, and nest stage. The cyclic effect of hour was highly significant (s(hour): edf = 5.57, $F = 6.03$, $P < 0.001$; **Table 10; Figure 5**), and the model had an adjusted R^2 of 0.679. With ambient temperature held constant at its observed overall mean (27.41°C), predicted internal nest temperatures were lowest during the early morning, increased following sunrise, reached their highest values around midday to early afternoon, and subsequently declined toward evening.

The nest-type-specific diurnal-pattern model evaluated whether the shape of this daily internal-temperature pattern differed between enclosed and open-cup nests by including a difference smooth for open-cup nests. The difference smooth had very low effective degrees of freedom and was not statistically supported (*s*(hour: Open)): edf = 0.249, $F = 0.034$, $P = 0.288$; **Table 10**). The simpler model containing a common diurnal smooth was also better supported

than the nest-type-specific model by both AIC (952.73 vs. 954.72) and BIC (1033.58 vs. 1041.79) (**Table 11**). Thus, although the predicted internal temperature of open and enclosed nests differed in vertical position among nest stages, their temporal trajectories followed the same general diurnal shape.

Basis-dimension diagnostics for the type-specific model at $k = 10$ indicated some potential sensitivity to the chosen basis dimension; therefore, the model was refitted with $k = 15$ as a sensitivity analysis. Increasing the basis dimension did not alter the biological conclusion: the nest-type-specific difference smooth remained effectively reduced to zero and unsupported (edf < 0.001, $P = 0.333$). The $k = 15$ type-specific model also received slightly less AIC support than the corresponding $k = 10$ model (955.68 vs. 954.72), further indicating that increasing spline flexibility did not improve the model. Residual diagnostics indicated that the ARMA(1,1) structure effectively accounted for most remaining short-term temporal autocorrelation, with lag-1 normalized residual correlations of approximately 0.038 for the thermal-offset model and 0.021 for the internal-temperature model.

4.2.2 Generalized Least-Squares Model Analysis

Generalized least-squares model analysis quantified the effects of nest type, nest stage, and microhabitat characteristics on thermal offset. The final generalized least-squares model incorporated an ARMA(1,2) temporal correlation structure with stage-specific residual variance and no additional nest-level random intercept. Allowing residual variance to differ among nest stages substantially improved model fit relative to a homogeneous-variance structure ($P <$ 0.001), indicating that residual variability differed significantly among nest stages. Final

statistical inference was based on CR2 cluster-robust variance estimates at the nest level with Satterthwaite small-sample degrees-of-freedom corrections.

Model selection indicated that no single model was best. Instead, six candidate models were considered competitive predictors of nest thermal offset (ΔAIC < 2; **Table 12**), all of which included an interaction between nest type and nest stage to predict thermal offset, and all but one competitive model also included additional covariates, such as canopy density, nest height, or clutch size. The top-ranked, most parsimonious competitive model included only the interaction between nest type and nest stage (ΔAIC = 0, w_i = 0.218) and was retained for inference. The additive model containing nest type and stage without their interaction received substantially less support (ΔAIC = 9.11), indicating greater model support for stage-dependent differences between nest types.

Although model selection favoured the inclusion of the interaction between nest type and nest stage, the overall interaction did not reach conventional statistical significance under the CR2 small-sample joint test ($F_{2, 3.35}$ = 5.93, P = 0.079). As a result, there was insufficient evidence that differences in thermal offset between open and enclosed nests varied among nest stages. While the individual coefficient for the open-nesting and nestling-stage interaction trended positive (β = 4.97, SE = 1.29, t = 3.85, df = 2.98, P = 0.031; **Table 13**), this localized effect must be interpreted with caution given the non-significant global joint test. Furthermore, direct stage-specific pairwise comparisons did not provide evidence of differences between nest types after Holm correction for multiple comparisons.

During incubation, open nests had an estimated thermal offset 1.50°C lower than enclosed nests (estimated difference = -1.50°C, 95% CI: [-3.80, 0.81], Holm-adjusted P = 0.301;

Table 14). During the empty stage, thermal offset was nearly identical between nest types, with open nests estimated to be 0.07°C lower than enclosed nests (estimated difference = -0.07°C, 95% CI: [-4.04, 3.90], Holm-adjusted $P = 0.939$). During the nestling stage, the direction of the difference was reversed, with open nests having an estimated thermal offset 3.48°C higher than enclosed nests; however, uncertainty around this estimate was substantial (estimated difference = 3.48°C, 95% CI: [-1.06, 8.01], Holm-adjusted $P = 0.235$). Model-estimated thermal offsets and their CR2 95% confidence intervals across the nest type and nest stage interaction combinations are shown in **Figure 6**.

Overall, thermal offset did not differ significantly between open and enclosed nests within any nest stage. Although the estimated differences varied in magnitude and direction among stages, all 95% confidence intervals included zero, indicating substantial uncertainty in the nest-type effects.

4.3 Nest Site Characteristics and Predator Observations

4.3.1 Nest Site Characteristics

Substrate type was not retained in the final nesting success models, but several notable descriptive patterns were observed:

Nest Height and Nest Type- Open-cup and enclosed nests differed significantly in their nest heights, with open-cup nests constructed at greater heights (median = 4.7 m, IQR = 4.2 - 7.4) than enclosed nests (median = 2.9 m, IQR = 2.0 - 3.6) (**Table 4**; **Figure 2b**).

Nest Height and Guild - Nest height varied among feeding guilds (ANOVA: $F = 38.86$, $p < 0.001$). Insectivorous species nested at greater heights than all other guilds ($p < 0.001$), while

omnivores occupied intermediate positions and nested higher than both granivores and nectarivores ($p < 0.001$). No difference in nest height was observed between granivores and nectarivores ($p = 0.82$).

4.3.2 Observations of Nest Failures, Predators, and Brood Parasitism

Confirmed nest predation events were documented for two nests during the 2023 field season. A trail camera at the Upper Agroforest Site recorded an invasive small Indian mongoose depredating an enclosed Bananaquit nest. The second event involved a native Grenada tree boa observed inside an open-cup nest after consuming its contents. The causes of the remaining nest failures could not be confirmed.

Two additional nest failures at the Upper Agroforest Site during the 2023 field season showed evidence potentially consistent with predation, although the causes could not be confirmed because of trail-camera malfunction or unsuccessful camera deployment. In one instance, a Bananaquit nest containing three nestlings too young to fledge was subsequently found empty, with a hole in the nest roof. The trail camera monitoring this nest malfunctioned approximately 24 hours before the nest failure, preventing determination of the cause. A Spectacled Thrush nest located along a pathway frequently used by mongooses failed during incubation. The cause of failure could not be confirmed because the substrate supporting the trail camera became unstable and shifted the camera away from the nest.

Potential nest predators were frequently detected by ground-level trail cameras during the 2023 field season and through direct field observations during both the 2023 and 2025 seasons. Trail cameras at the Upper Agroforest Site frequently recorded cats, mongooses, manicous

(opossums), and dogs travelling through the forest. Mongooses were also observed climbing trees and investigating active nests from distances of less than 5 m; several of these nests subsequently failed, although the causes of failure could not be determined because suitable locations for trail-camera installation were unavailable. Defensive behaviours toward potential nest predators were also observed during both field seasons. Tropical Mockingbirds aggressively mobbed and chased potential predators approaching active nest sites. During the 2023 field season, this behaviour was observed toward a Barbour's tropical racer (*Mastigodryas bruesi*), and in 2025 toward a small Indian mongoose, both at the Lower Semi-Natural Site. Gray Kingbirds were also observed mobbing and aggressively defending nests against Tricoloured Herons (*Egretta tricolor*), Antillean Broad-winged Hawk, cats, and humans.

Brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*) was recorded in three Tropical Mockingbird nests in 2023 and one Tropical Mockingbird nest in 2025, all at the Lower Semi-Natural Site. The 2025 nest was the same nest at which an adult Tropical Mockingbird was observed chasing a mongoose from the nest site. This nest contained five eggs, including two Shiny Cowbird eggs, and failed near the end of the incubation period.

4.3.3 Qualitative Observations of Invertebrate and Parasitic Activity

Two instances of ectoparasitism were recorded in nests. Ants were observed shortly after the conclusion of every breeding attempt in which nest contents remained, following either nest failure or successful fledging.

In 2025, severe mite infestations by mites (*Dermanyssus spp*.) were observed in two enclosed nests at the Lower Semi-Natural Site. A Grenada Wren nest in an anthropogenic structure failed after a mass infestation, with nestlings exhibiting lethargy and spasms before succumbing. Parents attempted two subsequent nest-building efforts within a 3-m radius, both of which were abandoned. Large numbers of mites were also observed in a successful Bananaquit nest following fledging, indicating that a substantial parasite load remained within the nest structure after the brood departed. A mite sample was collected and identified to the genus *Dermanyssus* by wildlife veterinarian Dr. Kenrith Carter.

In 2023, substantial ant activity was observed at three active Bananaquit nests, two at the Upper Agroforest Site and one at the Lower Semi-Natural Site. At the Upper Agroforest Site, ants were observed feeding on dead hatchlings. Whether the ants contributed to mortality or scavenged the hatchlings following death could not be determined. One Bananaquit nest located 3.6 m above ground in a mango tree was heavily colonized by ants morphologically consistent with fire ants (*Solenopsis spp.*). At the preceding nest check, two of three eggs had recently hatched, and the hatchlings appeared newly emerged and lacked developed down. Three days later, large numbers of ants were present throughout the nest, and only one hatchling carcass could be distinguished using the endoscope camera. A second Bananaquit nest, located 0.85 m above ground in a cocoa tree, was occupied by a smaller, light reddish-brown ant species that could not be identified. Ants were observed swarming throughout the nest and over all three dead hatchlings.

At the Lower Semi-Natural Site, a Bananaquit nestling, estimated to be approximately 14 days old based on nest-monitoring data, was found alive on the ground beneath its nest, located 2.9 m above ground in a mango tree. A swarm of ants morphologically similar to those observed at the mango-tree nest at the Upper Agroforest Site covered the nestling. A site worker removed the nestling from the ants. No specimens were collected from any of the 2023 ant observations; consequently taxonomic identification could not be confirmed.

Table 5. Species- and nest-level summary of the dataset used in the logistic-exposure analysis of nesting success during the 2023 field season. Nests are grouped by nest type (open, enclosed), with the number of nests monitored (*n*), successful and unsuccessful nests, median nest height (m), and median canopy density (%) reported for each species. Interquartile ranges are shown in parentheses.

Species	Nests	Successful	Unsuccessful	Nest Height	Canopy Density
Open Nest					
Common Ground Dove (*Columbina passerina*)	1	1	0	8.4 (8.4-8.4)	5.3 (5.3-5.3)
Eared Dove (*Zenaida auriculata*)	3	3	0	4.6 (4.6-4.6)	25 (24-28)
Gray Kingbird (*Tyrannus dominicensis*)	8	8	0	9.5 (5.4-10)	27 (20-36)
Tropical Mockingbird (*Mimus gilvus*)	12	7	4	4.7 (2.5-5.3)	29 (25-35)
Lesser Antillean Tanager (*Stilpnia cucullata*)	1	1	0	3.9 (3.9-3.9)	29 (29-29)
Spectacled Thrush (*Turdus nudigenis*)	11	5	5	4.3 (3.9-4.6)	41 (24-56)
Yellow-bellied Elaenia (*Elaenia flavogaster*)	2	1	0	6.3 (3.2-6.3)	63 (33-63)
Total	**38**	**26**	**9**	**-**	**-**
Enclosed Nest					
Grenada Wren (*Troglodytes grenadensis*)	1	1	0	3.7 (3.7-3.7)	100 (100-100)
Black-faced Grassquit (*Melanospiza bicolor*)	7	4	2	2.04 (1.9-2.6)	33.3 (8-41)
Lesser Antillean Bullfinch (*Loxigilla noctis*)	5	1	3	3.2 (2.5-3.2)	34.7 (24-100)
Bananaquit (*Coereba flaveola*)	19	7	11	2.9 (2.3-4.3)	32.0 (24-48)
Total	**32**	**13**	**16**	**-**	**-**
Overall Total	**70**	**39**	**25**	**-**	**-**

Table 6. Model-selection results for logistic-exposure models evaluating variation in daily nest survival during the 2023 field season. Candidate predictors included nest type (open, enclosed), Site (Lower Semi-Natural Site and Upper Agroforest Site), nest height (m), canopy density (%), and Julian date (days since 1 April 2023). Models are ranked by Akaike's Information Criterion corrected for small sample size (AIC_c). *K* represents the number of estimated parameters, AIC_c is the difference in AIC_c relative to the top-ranked model, and w_i is the Akaike model weight.

Model	*K*	AIC_c	ΔAIC_c	w_i
Nest Type x Nest Height + Site	**5**	**184.7**	**0.00**	**0.338**
(Nest Type x Nest Height) + (Nest Type x Canopy Density) + Site	**7**	**186.1**	**1.40**	**0.167**
(Nest Type x Nest Height) + Site + Julian Date	**6**	**186.4**	**1.70**	**0.144**
(Nest Type x Nest Height) + (Nest Type x Julian Date) + Site	7	187.3	2.66	0.089
Nest Type + Site + Nest Height	4	187.5	2.78	0.084
Nest Height	2	188.4	3.74	0.052
Nest Type + Site + Nest Height + Canopy Density	5	188.9	4.21	0.041
Nest Type + Site + Nest Height + Canopy Density + Julian Date	6	190.2	5.51	0.022
Nest Type + Site	3	190.8	6.12	0.016
Site	2	191.8	7.12	0.010
Nest Type	2	192.3	7.60	0.008
Nest Type x Date	4	192.4	7.76	0.007
Nest Type + Canopy Density	4	192.7	8.05	0.006
(Nest Type + Canopy Density) + Site	5	192.7	8.08	0.006
(Nest Type + Julian Date) + Site	5	194.1	9.38	0.003
(Nest Type x Canopy Density) + Site + Julian Date	6	194.2	9.49	0.003
Nest Type + Site + Canopy Density + Julian Date	5	194.4	9.75	0.003
Null	1	196.2	11.56	0.001
Julian Date	2	197.4	12.77	0.001
Canopy Density	2	197.5	12.88	0.001

Table 7. Model-averaged parameter estimates from logistic-exposure models of daily nest survival during the 2023 field season. Estimates were obtained by full model averaging across competitive candidate models ($\Delta AIC_c < 2$). Predictors included nest height (m), canopy density (%), Julian Date (days since 1 April 2023), and Site (Lower Semi-Natural Site (L), Upper Agroforest Site (U)). β = coefficient estimate; SE = standard error; OR = odds ratio; CI = 85% confidence interval. Enclosed nests and the Upper Agroforest Site are the reference categories.

Coefficients	β	β_CI	SE	p-value	OR	OR_CI
(Intercept)	3.35	[2.82, 3.89]	0.372	< 2e-16	28.6	[16.8, 48.8]
Nest Type: Open	**1.00**	**[0.073, 1.93]**	**0.647**	**0.12**	**2.73**	**[1.08, 6.91]**
Site: L	**0.856**	**[0.182, 1.53]**	**0.468**	**0.068**	**2.35**	**[1.20, 4.61]**
Nest Height	0.152	[-0.491, 0.796]	0.448	0.73	1.16	[0.612, 2.22]
Nest Type: Open x Nest Height	**2.05**	**[0.565, 3.53]**	**1.03**	**0.047**	**7.75**	**[1.76, 34.1]**
Canopy Density	0.0154	[-0.272, 0.392]	0.120	0.90	1.06	[0.762, 1.48]
Nest Type: Open x Canopy Density	**-0.210**	**[-1.56, -0.0661]**	**0.443**	**0.64**	**0.443**	**[0.210, 0.936]**
Julian Date	-0.0288	[-0.442, 0.183]	0.116	0.80	0.879	[0.643, 1.20]

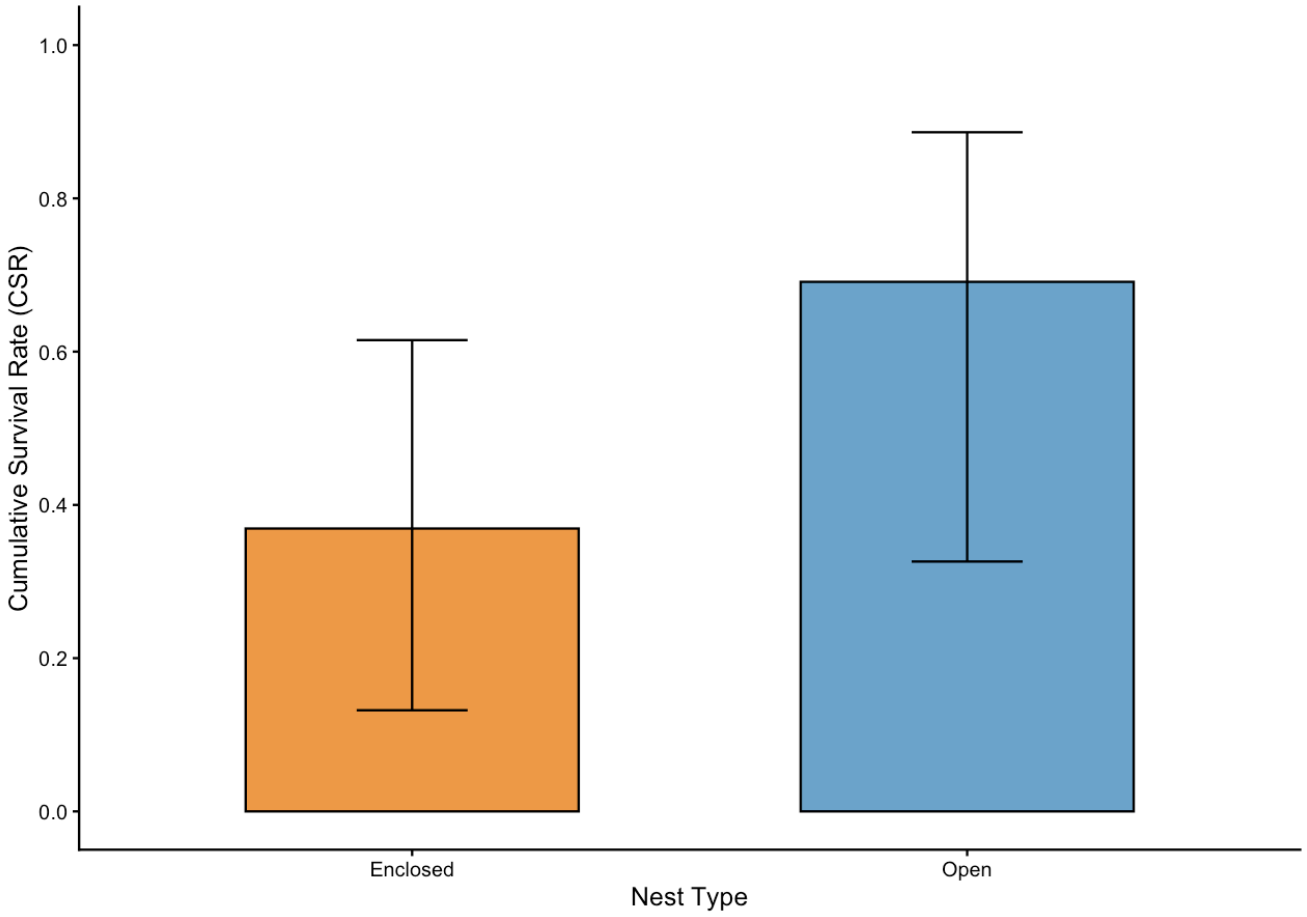

Figure 1. Cumulative survival rate (CSR) for open and enclosed nests during the 2023 field season derived from the logistic-exposure analysis. Predictions hold Julian date, canopy density (%), and nest height (m) at their mean values, and Site constant at the Upper Agroforest area. Error bars represent 95% confidence intervals.

Table 8. Model-averaged predicted daily survival rate (DSR) and 29-day cumulative survival rate (CSR) for open-cup and enclosed nests during the 2023 field season, derived from the logistic-exposure analysis. Values are presented with 95% confidence intervals.

Variable	DSR	CI_DSR	CSR	CI_CSR
Open-cup Nest	0.987	[0.962, 0.996]	0.691	[0.326, 0.886]
Enclosed Nest	0.966	[0.933, 0.983]	0.369	[0.132, 0.615]

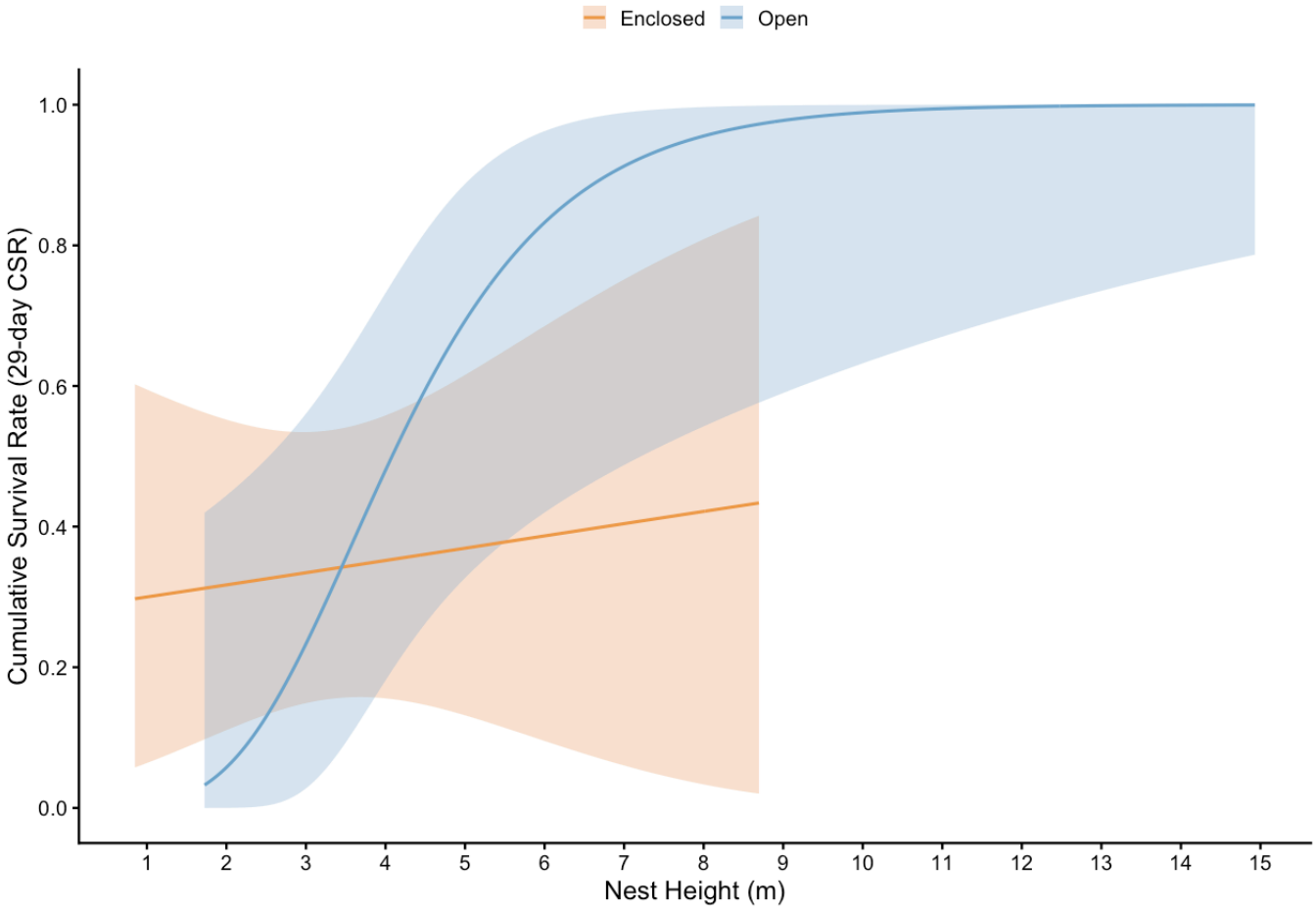

Figure 2. Cumulative survival rate (CSR) for open and enclosed nests across nest height (m) during the 2023 field season, derived from the logistic-exposure analysis. Predictions hold Julian date and canopy density (%) at their mean values, and Site constant at the Upper Agroforest area. Shaded areas represent 95% confidence intervals.

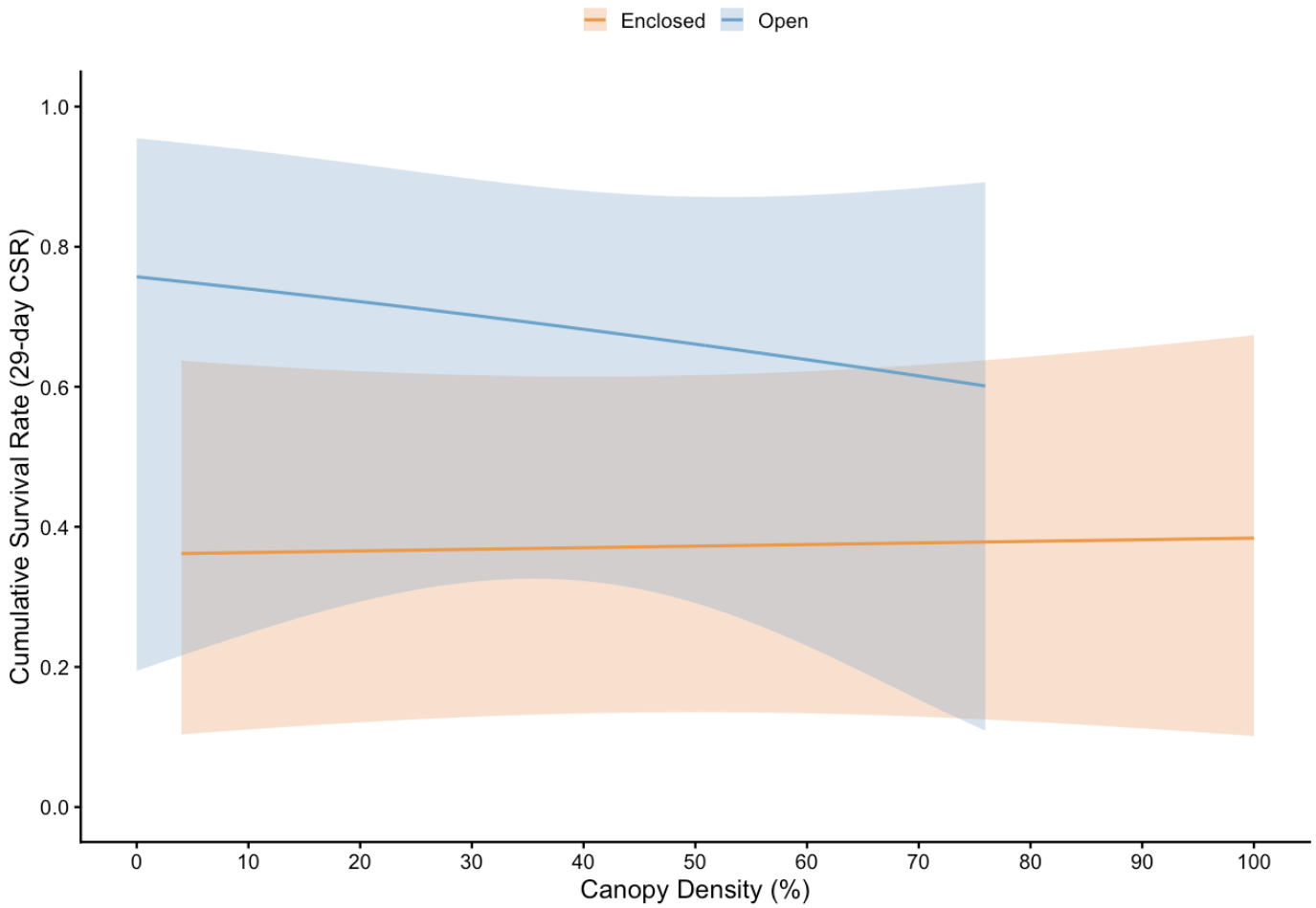

Figure 3. Cumulative survival rate (CSR) for open and enclosed nests across canopy density (%) during the 2023 field season, derived from the logistic-exposure analysis. Predictions hold Julian date and nest height (m) at their mean values, and site constant at the Upper Agroforest area. Shaded areas represent 95% confidence intervals.

Table 9. Species- and nest-level summary of the dataset used in the generalized additive mixed models and generalized least-squares model analyses of nest microclimate during the 2025 field season. Nests are grouped by nest type (open, enclosed), with the number of nests equipped with iButtons (*n*), median nest height (m), and median canopy density (%) reported for each species. Interquartile ranges are shown in parentheses.

Species	Nests	Nest Height	Canopy Density
Open Nesters			
Common Ground Dove (*Columbina passerina*)	1	2.7 (2.7-2.7)	55 (55-55)
Tropical Mockingbird (*Mimus gilvus*)	3	3.3 (2.4-3.9)	20 (17-36)
Spectacled Thrush (*Turdus nudigenis*)	1	3.0 (3.0-3.0)	39 (39-39)
Unknown_O	2	1.8 (1.7-1.8)	48 (33-63)
Total	**7**	**-**	**-**
Enclosed Nesters			
Black-faced Grassquit (*Melanospiza bicolor*)	1	1.5 (1.5-1.5)	0 (0-0)
Bananaquit (*Coereba flaveola*)	4	2.2 (1.1-3.1)	27 (22-31)
Unknown_C	1	1.3 (1.3-1.3)	28 (28-28)
Total	**6**	**-**	**-**
Overall Total	**13**	**-**	**-**

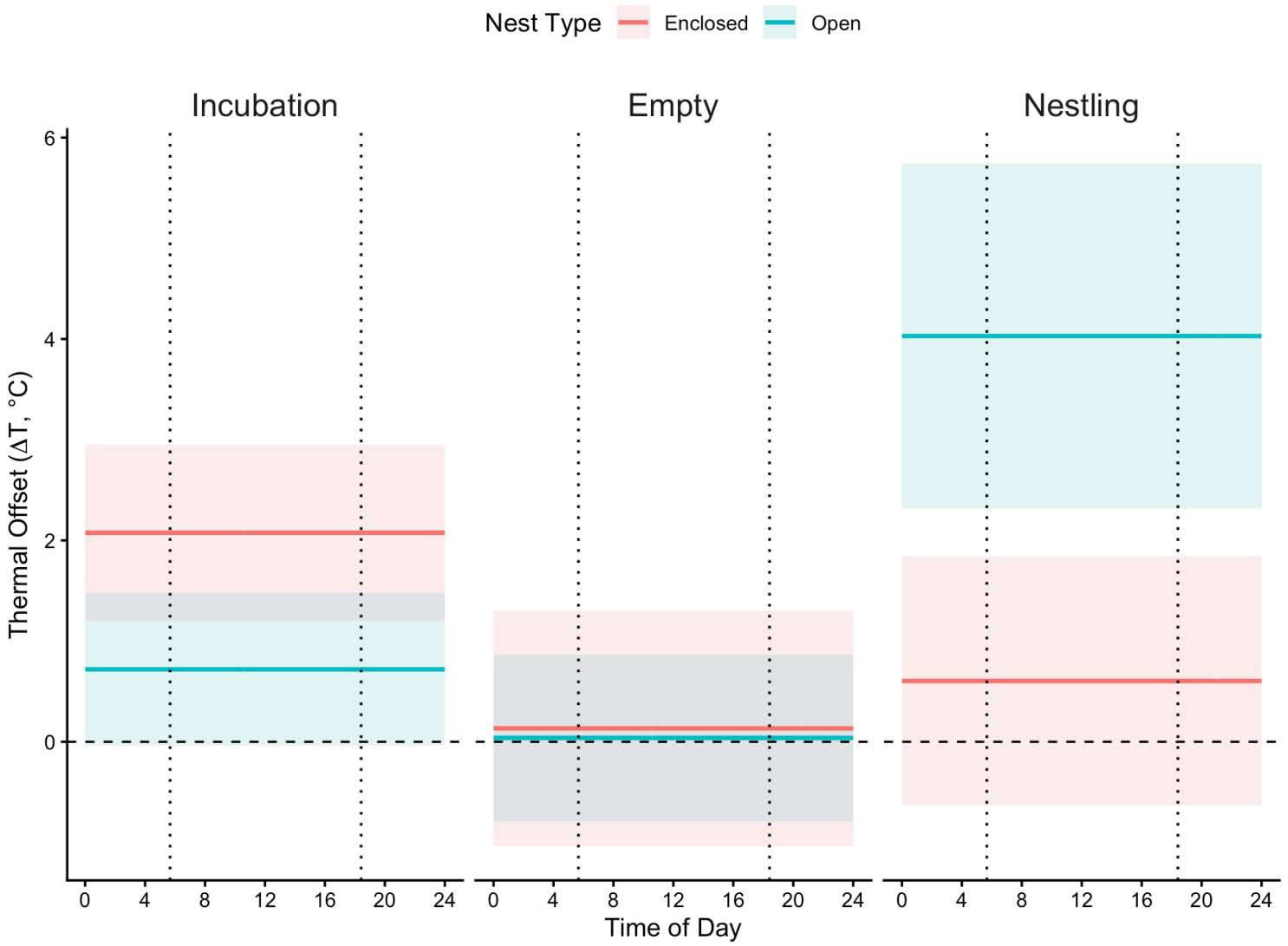

Figure 4. Generalized additive mixed model predictions of thermal offset ($\Delta T = T_i - T_a$; °C) across the 24-hour cycle for enclosed and open-cup nests during incubation, empty, and nestling stages in the 2025 field season. Predictions were derived from the final thermal-offset model. Shaded ribbons represent 95% confidence intervals. The horizontal dashed line at $\Delta T = 0$°C indicates equal internal nest (T_i) and ambient (T_a) temperatures. Dotted vertical lines indicate sunrise (05:40) and sunset (18:25).

Table 10. Smooth-term results from generalized additive mixed models used to evaluate diurnal variation in thermal offset ($\Delta T = T_i - T_a$; °C) and internal nest temperature (T_i; °C) during the 2025 field season. Cyclic cubic regression splines for hour of day (*s*(hour)) were used to model 24-hour temperature patterns, with a difference smooth for open-cup nests (*s*(hour): Open-cup) used to evaluate nest-type-specific diurnal variation.

Model	Smooth Term	Response Variable	edf	*F*	*P*
Thermal offset	s(hour)	ΔT	<0.001	<0.001	0.688
Internal temperature	s(hour)	T_i	5.57	6.03	**<0.001**
Nest-Type-specific diurnal pattern	s(hour)	T_i	5.57	5.79	**<0.001**
	s(hour): Open	T_i	0.249	0.0340	0.288

Table 11. Comparison of generalized additive mixed models evaluating whether the diurnal pattern in internal nest temperature (T_i; °C) differed between open-cup and enclosed nests during the 2025 field season. The internal-temperature model included a common diurnal smooth for both nest types, whereas the nest-type-specific diurnal-pattern model additionally included a difference smooth for open-cup nests. *K* represents the number of estimated parameters; AIC = Akaike's Information Criterion; BIC = Bayesian Information Criterion.

Model	K	AIC	BIC
Thermal offset	**13**	**952.73**	**1033.58**
Nest-Type-specific diurnal pattern	14	954.72	1041.79

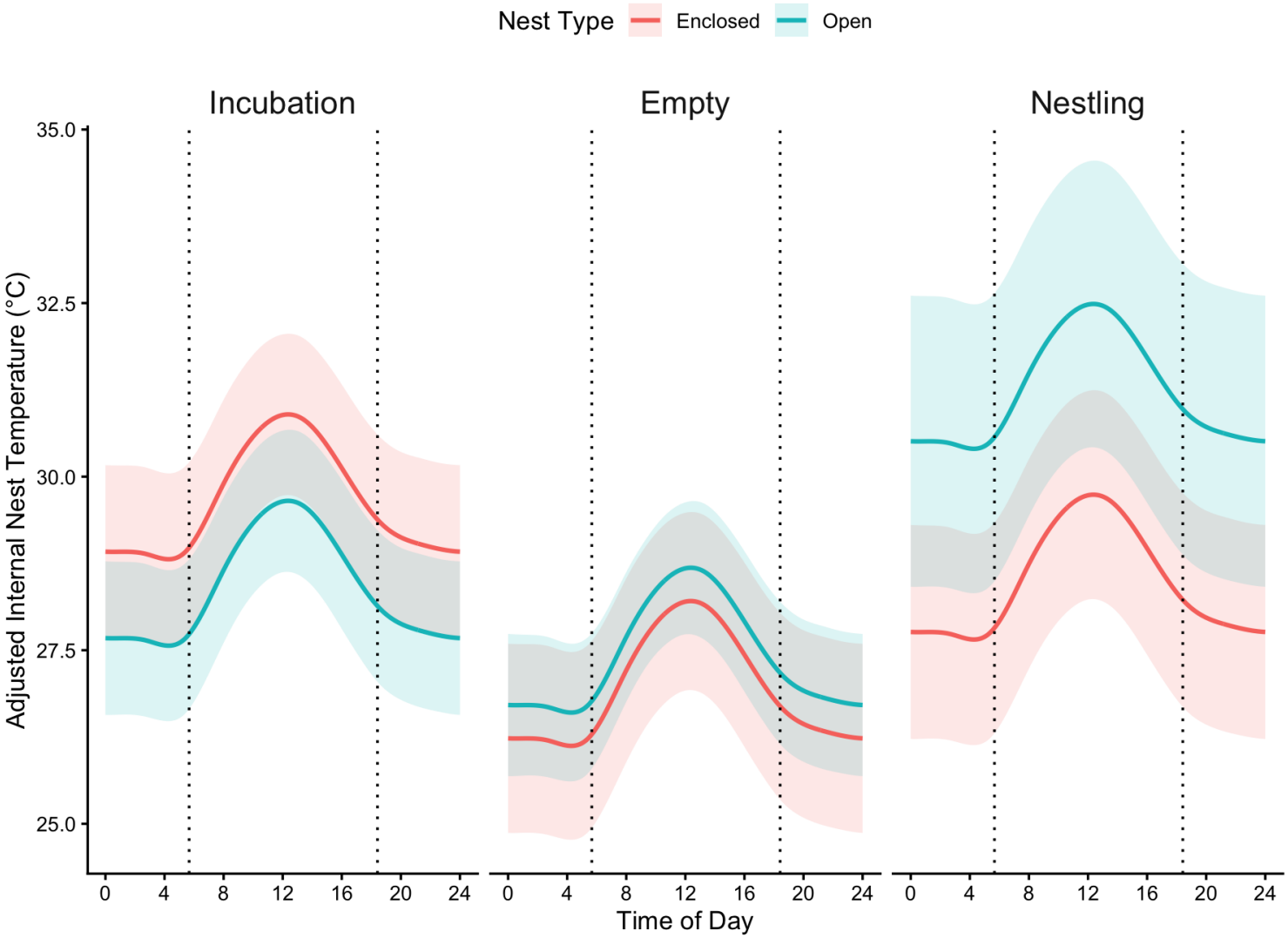

Figure 5. Generalized additive mixed model predictions of adjusted internal nest temperature (T_i; °C) across the 24-hour cycle for enclosed and open-cup nests during incubation, empty, and nestling stages in the 2025 field season. Predictions were derived from the final internal-temperature model, with ambient temperature (T_a) held constant at its observed overall mean (27.41°C). Shaded ribbons represent 95% confidence intervals. Dotted vertical lines indicate sunrise (05:40) and sunset (18:25).

Table 12. Model-selection results for generalized least-squares models evaluating variation in nest thermal offset ($\Delta T = T_i - T_a$; °C) during the 2025 field season. Candidate predictors included nest type (open, enclosed), nesting stage (empty, incubation, nestling), nest height (m), canopy density (%), and clutch size. Models are ranked by Akaike's Information Criterion corrected for small sample size (AIC_c). *K* represents the number of estimated parameters, AIC_c is the difference in AIC_c relative to the top-ranked model, and w_i is the Akaike model weight.

Model	*K*	AIC	BIC	ΔAIC	w_i
(Nest Type x Nest Stage)	**12**	**1899**	**1974**	**0.00**	**0.218**
(Nest Type x Nest Stage) + Clutch Size	**13**	**1900**	**1981**	**0.37**	**0.181**
(Nest Type x Nest Stage) + Canopy Density	**13**	**1900**	**1981**	**0.69**	**0.154**
(Nest Type x Nest Stage) + Nest Height	**13**	**1901**	**1982**	**1.39**	**0.109**
(Nest Type x Nest Stage) + Nest Height + Clutch Size	**14**	**1901**	**1988**	**1.42**	**0.107**
(Nest Type x Nest Stage) + Canopy Density + Clutch Size	**14**	**1901**	**1988**	**1.61**	**0.098**
(Nest Type x Nest Stage) + Canopy Density + Nest Height	14	1902	1989	2.5	0.063
(Nest Type x Nest Stage) + Canopy Density + Nest Height + Clutch Size	15	1902	1996	3.11	0.046
Clutch Size	8	1906	1955	6.24	0.010
Nest Stage	9	1907	1963	7.38	0.005
Canopy Density	8	1908	1958	8.85	0.003
Nest Type + Nest Stage	10	1908	1971	9.11	0.002
Null	7	1909	1952	9.43	0.002
Nest Type	8	1910	1960	10.70	0.001
Nest Height	8	1911	1960	11.30	<0.001

Table 13. Parametric coefficients from generalized additive mixed models used to evaluate the effects of nest type and nest stage on thermal offset ($\Delta T = T_i - T_a$; °C) and internal nest temperature (T_i; °C) during the 2025 field season. The internal-temperature model additionally accounted for ambient temperature (T_a; °C) Enclosed nests and the incubation stage were the reference categories. Thermal offset was calculated as $\Delta T = T_i - T_a$. β = coefficient estimate; SE = standard error.

Coefficient	*β*	SE	*t*-value	*p*-value
Thermal Offset Model				
Intercept	2.076	0.446	4.658	< 0.001
Nest Type: Open	-1.357	0.590	-2.301	0.021
Nest Stage: Empty	-1.943	0.745	-2.608	0.009
Nest Stage: Nestling	-1.472	0.773	-1.905	0.057
Nest Type: Open x Nest Stage: Empty	1.262	0.939	1.343	0.179
Nest Type: Open x Nest Stage: Nestling	4.782	1.229	3.891	< 0.001
Internal Temperature Model				
Intercept	19.250	0.756	25.447	<0.001
Ambient Temperature	0.379	0.017	21.699	<0.001
Nest Type: Open	-1.245	0.767	-1.624	0.104
Nest Stage: Empty	-2.689	0.865	-3.108	0.002
Nest Stage: Nestling	-1.156	0.947	-1.221	0.222
Nest Type: Open x Nest Stage: Empty	1.725	1.099	1.570	0.117
Nest Type: Open x Nest Stage: Nestling	3.992	1.491	2.677	0.007

Table 14. Stage-specific differences in nest thermal offset ($\Delta T = T_i - T_a$; °C) between open-cup and enclosed nests estimated from the generalized least-squares model during the 2025 field season. Positive estimates indicate greater thermal offset in open-cup nests, whereas negative estimates indicate greater thermal offset in enclosed nests. CR2 SE = cluster-robust standard error. *P*-values were adjusted for multiple comparisons using the Holm method.

Stage	Open - Enclosed	CR2 SE	95% CI	Holm P
Incubation	-1.5	0.86	[-3.80, 0.81]	0.301
Empty	-0.07	0.83	[-4.04, 3.90]	0.939
Nestling	3.48	0.96	[-1.06, 8.01]	0.235

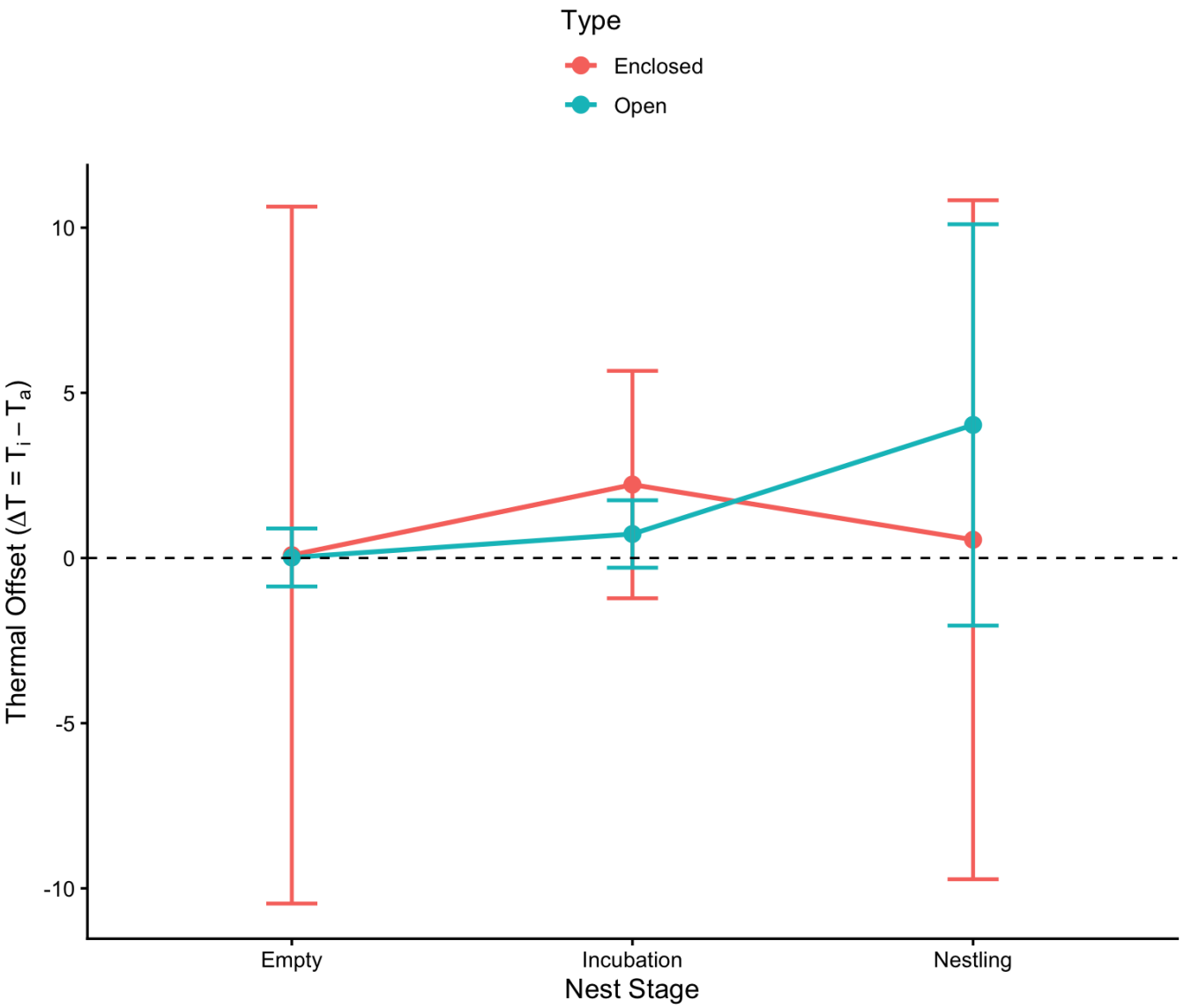

Figure 6. Generalized least-squares estimated nest thermal offset ($\Delta T = T_i - T_a$; °C) for enclosed and open nests across empty, incubation, and nestling stages during the 2025 field season. Points represent model-estimated mean thermal offsets, and error bars represent CR2 cluster-robust 95% confidence intervals with Satterthwaite small-sample degrees-of-freedom correction. The dashed horizontal line indicates $\Delta T = 0$ °C, where internal nest temperature (T_i; °C) equals ambient temperature (T_a; °C). Positive values indicate that internal nest temperatures were warmer than ambient conditions.

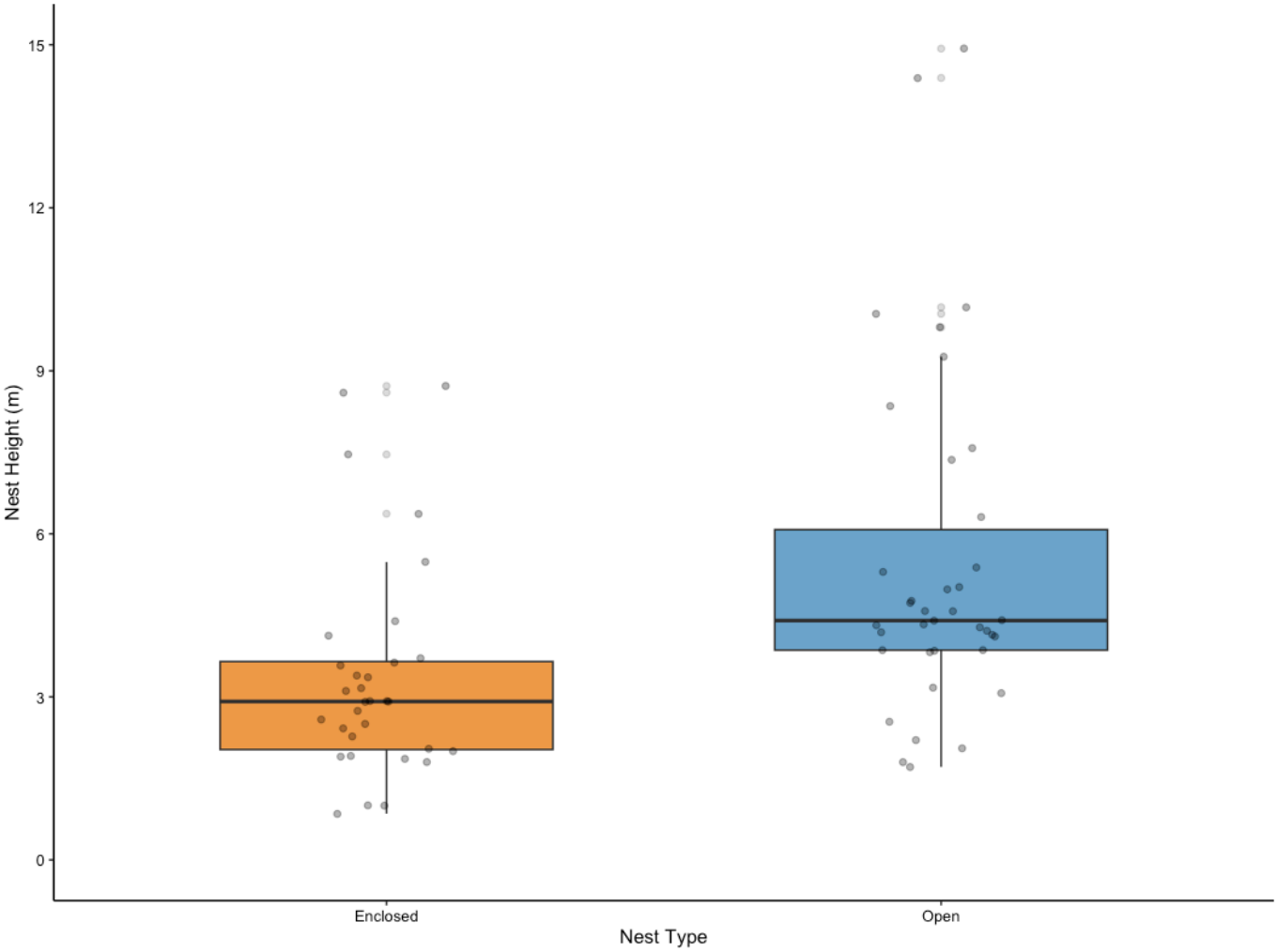

Figure 7. Distribution of nest height (m) for open-cup and enclosed nests of 11 native landbird species in Grenada during the 2023 field season. Nest height values represent the median height recorded for each unique nest (NID). Box plots show the median, interquartile range (IQR), and range, while individual points represent individual nests.

Chapter 5: Discussion

5.1 Nesting Success (2023)

5.1.1 Nest Structure and Nesting Success

In this study, I investigated nesting success across 11 resident landbirds in Grenada in relation to nest structure, microhabitat, and time within the breeding season. Open-cup nests exhibited substantially higher cumulative survival than enclosed nests (69.1% vs. 36.9%). This result suggests that nest structure plays an important role in mediating nest survival in this system. This pattern is consistent with the literature and provides support for the benefits of open-cup nests (Vanadzina et al., 2024; Martin et al., 2017; Medina et al., 2022). The higher success of open-cup nests may be attributed to a variety of factors, such as an unobstructed field of view, which allows parental birds to detect predators early and execute rapid escape or defensive responses, species-specific traits, habitat structure, and the local predator community (Götmark et al., 1995; Price & Griffith, 2017; Weidinger, 2002). This distinction is important because nest type is a species-level characteristic rather than a trait that is randomly distributed among nests (Medina et al., 2022; Sheard et al., 2024). Nest architecture therefore covaries with other ecological characteristics, including body size, feeding guild, typical nest height, habitat use, and parental behaviour. Consequently, the observed difference between open-cup and enclosed nests likely represents the combined influence of several correlated traits rather than the isolated effect of nest architecture. The persistence and high diversity of enclosed nesting strategies in tropical bird communities further demonstrate that enclosed nests must provide benefits under at least some ecological conditions (Mainwaring et al., 2014; Martin et al., 2017).

Body size is also important to consider when interpreting results. Species that typically build open-type nests tend to be larger in size. Larger-bodied birds benefit from building open-cupped nest structures, with sturdier bases that support adult and developing nestling mass (Deeming & Mainwaring, 2015). Larger birds are also more aggressive and are known to fend off a more diverse range of nest predators than smaller species. Furthermore, they can defend their nests more effectively against a wider variety of predators (Unzeta et al., 2020). Unzeta et al. (2020) found a consistent decrease in daily nest predation rate with increasing body size, even after accounting for regional, phylogenetic, and year effects, and it remained constant after removing the effect of exotic nest predators. Gray Kingbirds and Tropical Mockingbirds exhibited behaviours supporting those inferences, including active nest defence such as mobbing, facultative breeding, and mate guarding, all of which reduce predation risk despite increased exposure and the extra energetic costs, and enhance nesting success (Hansell, 2000; Medina et al., 2022; Mouton & Martin, 2019; Stutchbury & Morton, 2001). Gray Kingbirds, in particular, were frequently observed aggressively chasing off potential predators, including Broad-winged Hawks, which likely contributed to the fact that all monitored nests for this species were successful (Campbell, 2019).

While enclosed structures provide physical concealment and prevent visual detection of nest contents, they trade off the adaptive advantages of open-cup nests. For instance, this study confirmed only two predator events, and one involved a mongoose predating a conspicuous, bulky Bananaquit nest. This pattern aligns with a growing body of evidence indicating that enclosed nests do not consistently experience lower predation than open-cup nests and that open-

cup nests can outperform enclosed structures under specific ecological conditions (Martin et al., 2017; Mouton & Martin, 2019).

The structural nature of enclosed nests allowed these species to utilize a broader range of substrates, including vines and anthropogenic features. Open-cup nesters, conversely, were more restricted to stable substrates like trees, palms, and shrubs. However, open-cup nests are often constructed with fewer materials and are smaller relative to the builder, resulting in lower time and energy costs (Hansell, 2000; Medina et al., 2022; Mouton & Martin, 2019). This suggests a fundamental trade-off: enclosed nesters achieve a broader niche breadth in nest-site selection, yet this flexibility does not translate into higher success.

5.1.2 Microhabitat Effects in Nest Site Selection

Nest Height- The higher survival rates observed at greater nest heights, particularly for open-cup nests, likely reflect a shift in predation pressures associated with the introduction of invasive ground predators (Matysioková & Remeš, 2024; VanderWerf, 2012). In this system, the higher survival of open-cup nests may indicate that behavioural strategies, such as increased vigilance and rapid predator detection, likely outweigh the structural advantages of enclosed nests (Lima, 2009). Enclosed nests exhibited comparatively little change in survival across their observed height range, indicating that lower placement alone does not fully explain the reduced survival in enclosed-nesting birds.

In tropical systems, where predator communities include both terrestrial and arboreal species, the relationship between nest height and survival is often more variable and context-dependent (Ibáñez-Álamo et al., 2015; Matysioková & Remeš, 2024). In this study, the

relationship between nest height and survival differed between nest structures, with survival increasing more strongly with height among open-cup nests while changing comparatively little among enclosed nests. This pattern supports the broader hypothesis that the survival consequences of nest placement are contingent upon both nest architecture and the composition of the predator community within a system (Borgmann et al., 2013; Ibáñez-Álamo et al., 2015). Larger-bodied open-cup nesting species may better defend their nests against a broader range of aerial and arboreal predators, potentially allowing them to tolerate the risks of nesting higher in the vegetation strata if doing so reduces exposure to invasive ground-based predators. Thus, greater nest height may reflect a trade-off between predator guilds, whereby open-cup nesters reduce vulnerability to terrestrial predators at the potential cost of increased exposure to native predators occupying higher vegetation strata (Ibáñez-Álamo et al., 2015; Matysioková & Remeš, 2024). This pattern may suggest that nesting strategies in Grenada could be responding to a shifting predator regime, where previous adaptive behaviours are being reshaped by the presence of invasive species, suggesting a trade-off between predator types. Although historical data are unavailable to determine whether nest heights have shifted in Grenada, similar changes in nesting behaviour following predator introductions have been documented in other island systems. For example, in the Hawaiian archipelago, the introduction of invasive black rats forced native open-cup nesting species such as the Oahu Elepaio (*Chasiempis ibidis*) to modify their nesting strategies and build nests significantly higher in the canopy to escape more vulnerable understory layers (VanderWerf, 2012). Similarly, in the Galápagos, Medium Tree Finch (*Camarhynchus pauper*) had predator- and nest-height-specific risks. Lower nests were suspected to have experienced greater predation by introduced black rats, whereas higher nests

experienced greater avian predation, demonstrating how vulnerability to different predator guilds can vary across vertical nesting strata (Kleindorfer et al., 2021).

An additional consideration when interpreting the relationship between nest structure and nest height is the difficulty of monitoring enclosed nests at greater heights. Enclosed nests of species such as Bananaquits and Lesser Antillean Bullfinches were observed nesting high in the palm nuts of king palm trees, including many of which were approximately 15 m. At these heights, the enclosed structure made it difficult, almost impossible, to reliably determine nest contents, stage, and fate from the ground. In contrast, open-cup nests at similar heights were generally easier to assess visually due to their open structure and the larger size of the nesting species. As a result, the monitored sample contained fewer high enclosed nests than occur within the nesting community. Greater height may be sufficient to reduce encounters with terrestrial and lower-stratum predators. For example, although ground predators like mongooses and cats are highly adaptable and capable climbers, increasing nest height may reduce nest accessibility and increase the energetic cost of reaching the nest enough that the trade-off of the amount of energy required to reach and depredate the nest is no longer profitable compared to more optimal and accessible understory prey (Key et al., 1998; Schmidt, 1999).

Canopy Density- Canopy density influenced nesting success, but, contrary to the predicted effect, vegetation cover did not enhance nest survival through improved concealment. Results indicated that increased canopy density, or nest concealment, was associated with reduced survival for open-cup nests, while having little to no effect on enclosed nests. Although dense vegetation can reduce nest conspicuousness, it may also create conditions that favour predators

by concealing their movements and obstructing nesting birds' visual field (Remeš, 2005; Weidinger, 2002). This may be particularly relevant for predators that do not rely on visual cues to detect nests. For example, Grenada tree boas are arboreal, nocturnal predators that can locate prey using non-visual sensory cues, including olfactory and thermal information, effectively making them excellent ambush predators (Henderson, 2019; Henderson et al., 2009). Greater canopy density may therefore come with a trade-off between nest concealment and predator detection.

Interestingly, the lack of relationship between canopy density and enclosed nests is perhaps because their structural concealment already provides a degree of protection independent of surrounding vegetation. Consequently, these nests may be less influenced by variation in canopy cover and instead reflect other selective pressures, such as thermoregulation or microclimate stability (Mainwaring et al., 2014). Additionally, native predators in Grenada are generally considered opportunistic, with birds comprising a relatively small component of their diet (Campbell, 2019; Henderson & Pauers, 2012; Pérez-Rivera, 2020). As such, predation pressure from these species may be sporadic and context-dependent. In contrast, invasive ground-based predators may impose more consistent predation risk in lower strata. Under these conditions, nesting at greater heights may represent a trade-off, where exposure to arboreal predators is offset by reduced risk from terrestrial predators, ultimately resulting in higher overall survival. Interpretation of the canopy density response should also consider the limited species-level replication within each nest structure, with only four enclosed-nesting species compared with seven open-cup species. Consequently, some of the observed differences may reflect species-specific habitat use rather than nest architecture alone. This limited replication also

introduces a potential phylogenetic confound, as nest architecture is deeply conserved within lineages, making it difficult to separate structural effects from shared evolutionary traits (Fang et al., 2018; Winkler & Sheldon, 1993). For example, Black-faced Grassquits nested particularly low at a median height of 2.04 m (1.9-2.6) and often used dense or structurally defensive substrates such as cacti and pineapple plants, which may provide protection despite limited surrounding concealment (Raffaele et al., 2020; Wetmore & Swales, 1931). Their low nest placement may also reflect their granivorous foraging ecology, as they typically feed close to the ground in grasses and sedges (Raffaele et al., 2020; Wunderle, 1985). More broadly, the weak relationship between canopy density and survival among enclosed nests may reflect both the structural concealment provided by the nest itself and their generally lower vertical placement. Thus, canopy density may not represent the same immediate habitat conditions or predator exposure for open-cup and enclosed nests, and the observed interaction likely reflects a combination of nest architecture, nest height, and species-specific habitat use. The weak effect among enclosed nests therefore cannot be confidently attributed solely to their architecture. Furthermore, the comparatively weak relationships between survival and either nest height or canopy density among enclosed nests should not necessarily be interpreted as evidence that microhabitat characteristics are unimportant for these species. Rather, nesting success may depend on combinations of nest architecture and nest-site characteristics that were not adequately represented by the two-way interactions examined here (Borgmann et al., 2013). For example, the influence of nest height may depend simultaneously on nest architecture, vegetation density, predator accessibility, and species-specific behaviour. Evaluating such context dependence would require higher-order interactions among nest type, nest height, and canopy density.

However, the number of monitored nests, in particular, the limited replication for enclosed-nesting species and across combinations of microhabitat conditions, was not sufficient to reliably estimate such complex interactions. Consequently, the absence of strong individual effects of nest height and canopy density among enclosed nests should be interpreted cautiously rather than as evidence that these characteristics have no influence on nesting success.

Site- Nest survival was higher at the Lower Semi-Natural Site than at the Upper Agroforest Site, indicating that site-level habitat differences influenced reproductive success. This indicates that the broader habitat context plays an important role in shaping reproductive outcomes. Although Site was included as a control variable rather than a focal predictor, these differences provide important ecological insight into how habitat structure, human activity, and predator communities may interact to influence nesting success. The two study sites differed in vegetation structure, disturbance regimes, and landscape composition. The Lower Semi-Natural Site consisted of a more open, human-modified agro-garden matrix with regular vegetation maintenance, reduced understory density, and high levels of human activity. In contrast, the Upper Agroforest Site featured a denser, structurally connected agroforestry system with greater canopy cover, denser vegetation, and lower levels of human disturbance. Regular vegetation maintenance may also have reduced concealed movement pathways available to ground predators. However, it creates more edge habitats, which the Grenada tree boa thrive in (Henderson & Berg, 2011). This makes sense that one confirmed predation event by the tree boa occurred at the Lower Semi-Natural Site, in a roadside nest.

By contrast, the Upper Agroforest Site had greater structural connectivity and denser undergrowth, which likely served as protected travel corridors for invasive generalists. Field observations support this, with mongoose activity more prevalent at the Upper Agroforest Site along established trail networks, where several Spectacled Thrush nests failed despite being concealed in structurally complex vegetation. This suggests that, in this modified landscape, predation risk is driven more by predator accessibility and movement patterns than by microhabitat cover alone. Interestingly, this also tracks with the other confirmed predation event by a mongoose, which occurred at the Upper Agroforest Site in the cocoa and banana mixed agroforest portion. These observations highlight the presence of both invasive ground predators and native arboreal predators within the system. Additional field observations, including repeated detection of mongooses along movement pathways near active nests and instances of snakes occupying nesting vegetation, further support the inference that predation pressure is substantial.

Higher survival at the Lower Semi-Natural Site may reflect a human-shield effect, whereby frequent human activity indirectly reduces predation risk by deterring predators from otherwise suitable nesting habitat (Leighton et al., 2010; Muhly et al., 2011). Leighton et al. (2010), for example, found that introduced mongooses used areas of high human activity less frequently, resulting in corresponding reductions in estimated nest-predation risk. Regular human activity at the Lower Semi-Natural Site may therefore have provided nesting birds with some degree of indirect refuge from human-averse predators. At the same time, human-tolerant species such as Bananaquits, Lesser Antillean Bullfinches, and Grenada Wrens benefit from cultivated and anthropogenic environments by accessing flowering and fruiting plants and other food resources (Audet et al., 2016; De Ruyck, 2023). These species often forage close to humans and

exploit anthropogenic food subsidies (Audet et al., 2016; Ducatez et al., 2013). Increased access to predictable food resources may enhance the attractiveness of anthropogenic habitats as nesting areas, potentially increasing local bird activity and competition for suitable nest sites (Shochat et al., 2006). Consistent with this possibility, Bananaquits, Lesser Antillean Bullfinches, and Grenada Wrens were frequently observed competing aggressively for nest sites around the restaurant at the Lower Semi-Natural Site, with interactions between Lesser Antillean Bullfinches and Grenada Wrens occurring particularly frequently. All three species are enclosed nesters and were commonly observed nesting in anthropogenic structures at the site.

5.1.3 Temporal Effects: Seasonality and Breeding Phenology

Seasonal timing had a limited influence on nesting success, as Julian date was retained in the model but had a weak, non-significant effect. This suggests that while temporal variation was considered, it did not strongly influence survival relative to other predictors. Although seasonal changes were expected to affect nesting success through shifts in vegetation density, rainfall, and predator activity, we detected no clear temporal trends. This may be because the study duration could not capture sufficient seasonal variation (Robinson et al., 2000; Stutchbury & Morton, 2001). Additionally, active vegetation management at both sites may have reduced temporal changes in habitat structure. As a result, seasonal increases in vegetation density, which would typically influence concealment and predator dynamics, may have been dampened across both sites. Finally, the stronger influence of structural and spatial factors, particularly nest placement and predator accessibility, may have overridden more subtle temporal effects on nesting success (Borgmann & Conway, 2015).

5.2 Microclimate (2025)

The study also examined nest microclimate and whether thermal conditions varied in relation to nest architecture, reproductive stage, and surrounding microhabitat characteristics across five of the 11 species represented in the nesting-success component of the study. These comprised three open-cup nesting species and two enclosed-nesting species. Calculating thermal offset ($\Delta T = T_i - T_a$) provided a particularly useful measure of nest microclimate because it quantified the degree to which internal nest temperatures deviated from simultaneous ambient conditions.

5.2.1 Diurnal Pattern

Internal nest temperature exhibited a pronounced diurnal cycle, which was consistent with the expected variation in solar radiation and the corresponding ambient temperatures throughout the day (Deeming & Reynolds, 2015). However, the absence of a corresponding nonlinear pattern in thermal offset suggests that the difference between internal and ambient temperatures remained comparatively stable over the 24-hour cycle. This indicates that nests did not strongly modify thermal conditions relative to the surrounding environment across the daily cycle. Similarly, the absence of distinct diurnal thermal-offset trajectories between open-cup and enclosed nests suggests that enclosure did not fundamentally alter how nest temperatures responded to daily environmental variation.

Enclosed nests were expected to better offset temperatures because their walls and roofs can modify solar exposure, airflow, and convective heat exchange. If enclosure strongly moderated external temperature fluctuations, enclosed nests might have warmed more slowly as

ambient temperatures increased or retained heat longer as temperatures declined (Heenan & Seymour, 2012; Martin et al., 2017). Such differences were not evident in the present study, suggesting that both nest architectures remained strongly influenced by the surrounding thermal environment. This does not necessarily mean that nest structure had no effect on internal conditions. Rather, any structural influence was not sufficient to generate markedly different diurnal thermal trajectories under the conditions sampled.

This close correspondence between internal and ambient temperature is ecologically important because eggs and nestlings are confined to the nest and have limited ability to avoid unfavourable conditions during early development (Deeming & Reynolds, 2015; Nord & Giroud, 2020). Their thermal environment may therefore depend substantially on ambient conditions, particularly in tropical systems where high temperatures can approach physiological limits, and species may possess relatively narrow thermal breadths (Nord & Giroud, 2020; Visser, 1998). The strong coupling observed between nest and ambient temperatures therefore suggests that changes in the external thermal environment may be transmitted relatively directly to the conditions experienced within nests.

5.2.2 Nest Type and Stage Interaction

The relationship between nest architecture and thermal offset was more complex than originally predicted. I expected enclosed nests to show a consistently greater thermal offset than open-cup nests, with the magnitude of this effect varying by reproductive stage. However, the data did not support this prediction, as comparisons between nest types were not statistically significant at any nest stage (empty, incubation, nestling). Interestingly, the descriptive trends

revealed a shifting pattern: enclosed nests showed a greater positive thermal offset during incubation, which reversed during the nestling stage, when open-cup nests exhibited the larger positive thermal offset. The approximately 3.5°C difference between nest architectures during the nestling stage was particularly notable. Although this contrast was associated with broad uncertainty and cannot be interpreted as a confirmed population-level difference, its magnitude and reversal relative to incubation are noteworthy and may suggest that the thermal consequences of nest architecture may change as nests progress through the reproductive cycle.

This apparent shift may partly reflect the increasing contribution of biological activity within occupied nests. Developing nestlings produce metabolic heat, which can contribute increasingly to nest temperature as they grow (Ar & Sidis, 2001; Nord & Giroud, 2020). Consequently, the thermal environment during the nestling stage is not simply the product of heat exchange between the nest structure and its surroundings, but also reflects heat generated by the developing brood. Parental behaviour may further complicate these relationships. During incubation, prolonged adult attendance contributes directly to nest temperature, whereas during the nestling stage adults alternate among brooding, provisioning, and periods away from the nest. These behavioural transitions could change both the amount of heat introduced into the nest and the opportunities for that heat to dissipate (Conway & Martin, 2000; Mueller et al., 2019). Thus, the same nest architecture may function differently depending on its reproductive contents: an enclosed nest containing incubated eggs may have very different thermal properties from the same structure containing a growing, metabolically active brood (Deeming & Mainwaring, 2015; Maziarz et al., 2017). Likewise, the relatively large thermal offset observed in open-cup nests during the nestling stage may reflect the combined effects of architecture, brood heat production,

parental attendance, and heat dissipation rather than nest structure alone. The thermal consequences of nest architecture may therefore be dynamic rather than a fixed property of the structure itself.

Although these stage-specific differences were not statistically supported, their direction and magnitude suggest that reproductive stage may still be an important consideration when evaluating the thermal consequences of nest architecture. Rather than functioning independently, architecture and biological activity may interact to determine the thermal environment experienced within an occupied nest. Greater biological replication across nest architectures and reproductive stages will be required to determine whether the apparent reversal observed here represents a consistent population-level pattern.

5.2.3 Microclimate and Microhabitat Relationship

Nest microclimate was not significantly influenced by microhabitat characteristics such as nest height and canopy density, regardless of nest type or stage. Thus, neither greater canopy cover nor variation in nest height produced a detectable and consistent effect on thermal offset within the range of nests sampled. This contrasts with the expectation that nest-site microhabitat would modify exposure to solar radiation and other environmental heat sources. The absence of detectable effects suggests that the measured microhabitat variables explained little additional variation in nest-scale thermal conditions under the conditions sampled. Factors such as nest orientation, direct versus intermittent solar exposure, surrounding vegetation geometry, wind exposure, substrate characteristics, or the timing and duration of shading may influence nest temperatures in ways not captured by canopy density or nest height alone. Consequently, the lack

of significant relationships should not necessarily be interpreted as evidence that nest placement is thermally unimportant, but rather that the measured microhabitat characteristics did not explain substantial additional variation under the conditions represented in this dataset.

5.3 Limitations and Future Directions

5.3.1 Nesting Success (2023)

This study was conducted over a single field season and did not capture the full annual breeding cycle of Grenadian landbirds, many of which may breed over extended or near year-round periods. As a result, interpret estimates of nesting success and predictor effects within this limited temporal window, as short-term studies may not capture broader ecological variability (Roper, 2005; Thompson et al., 2001). Longer-term monitoring across multiple breeding seasons would help determine whether the relationships identified here remain consistent under different ecological conditions.

Species representation was also uneven across nest architectures. Enclosed nests were dominated largely by Bananaquits, whereas the open-cup sample contained substantial representation from Spectacled Thrushes. Consequently, some apparent differences between nest types may also incorporate differences in species-specific behaviour, nest placement, parental activity, or responses to human disturbance. For example, these species differ considerably in their behaviour and apparent tolerance of human activity around nesting areas, illustrating how nest architecture may be associated with broader species-specific life-history and behavioural strategies. Unequal sample sizes between open-cup and enclosed nests may have further resulted in differing statistical power between the two groups. Future studies with greater and more

balanced replication across nest architectures, and sufficient samples within individual species, would allow the effects associated with nest architecture and species identity to be distinguished more effectively.

Nest detection and accessibility imposed additional limitations. More conspicuous or accessible nests were more likely to be located and subsequently monitored, while nests positioned high in the canopy or within dense vegetation were harder to observe reliably. This limitation may have been particularly important for enclosed nests. Although monitored enclosed nests generally occurred at relatively low heights, enclosed nests were observed elsewhere in the study area at substantially greater heights that could not always be monitored consistently. The comparatively weak response of enclosed-nest survival to increasing nest height should therefore be interpreted only within the range of heights represented in the monitored dataset, rather than as evidence that nest height is biologically unimportant for enclosed-nesting species. Future analyses examining variation in nest height within individual species, particularly those represented by sufficiently large samples, could help determine whether individuals nesting higher also experience greater survival when species-level differences are held more constant.

Predator identification represented another important limitation. Most nest failures could not be attributed to a particular predator because relatively few predation events were directly observed. Although both native and invasive predators were documented interacting with nests, we could not quantify their relative contributions to nest failure. This also limited the ability to determine whether vulnerability to particular predators changed over the course of a nesting attempt. Exploratory observations suggested that failures may occur more frequently during the nestling stage under some circumstances, when parental provisioning and nestling activity could

increase visual, acoustic, or olfactory cues surrounding the nest, but this could not be determined with any certainty. Increased camera surveillance would substantially improve this aspect of future research. Further, using continuous video rather than motion-triggered photographs would be beneficial, providing a more complete record of predator movements and improving detection of small, rapid, or indirect interactions that may otherwise be missed. This would also allow predator approach behaviour, predator identity, and parental responses to be captured and analyzed.

More broadly, nesting success represents only one component of demographic performance and cannot by itself determine whether a habitat supports a self-sustaining population. Assessing population persistence requires information on juvenile recruitment, post-fledging survival, adult survival, dispersal, and movement among habitats. Future work in Grenada should therefore build upon the nesting-success data from this study by incorporating these additional demographic processes to determine whether populations occupying different habitats function as demographic sources or sinks (Pulliam, 1988; Donovan et al., 1995).

5.3.2 Microclimate (2025)

The microclimate component of this study was constrained primarily by the small number of instrumented nests and the duration and distribution of sampling. Each nest was generally monitored during a single 24-hour deployment, providing a detailed snapshot of thermal conditions but not the full range of conditions experienced throughout a breeding attempt or across the broader breeding season. Notably, iButton deployment may also not have

coincided with particularly hot, cool, wet, or otherwise stressful periods, limiting the ability to determine whether differences among nest architectures become more pronounced under environmental extremes. Data were collected at a single study site, further limiting inference about broader habitat-level variation in thermal conditions. In addition, sensor deployment was restricted to nests that were accessible and structurally suitable for instrumentation, potentially biasing the sample toward particular nest types, heights, or microhabitats.

The relatively small and uneven sample sizes among nest architectures and reproductive stages also limited statistical power, particularly for estimating interactions among nest type, stage, and environmental conditions. Although descriptive thermal patterns varied among nest architectures and reproductive stages, these differences were not statistically supported, and several estimates were associated with substantial uncertainty. Greater and more balanced replication across nest types, reproductive stages, species, and environmental conditions will therefore be necessary to determine whether these patterns occur consistently.

A further limitation is that nest architecture cannot be fully separated from the characteristics of the location where a nest is constructed. Internal nest temperature reflects not only whether a nest is open or enclosed, but also the environmental conditions immediately surrounding it. Although canopy density and nest height provided measures of microhabitat structure, these variables cannot fully characterize the thermal exposure experienced by an individual nest. Future studies would benefit from more direct measurements of solar radiation, shade duration, humidity, airflow, nest orientation, surrounding vegetation structure, substrate, and nest construction characteristics. Incorporating these variables would allow the mechanisms

underlying thermal variation to be evaluated more directly and help distinguish effects associated with nest architecture from those arising from nest placement and local environmental exposure.

Biological activity within the nest represents an additional source of thermal variation that cannot necessarily be attributed to architecture or microhabitat. Parental incubation and brooding, provisioning activity, brood size, nestling development, and metabolic heat production may all influence internal nest temperatures. Simultaneous behavioural and thermal monitoring would therefore help distinguish changes resulting from environmental exposure from those generated by biological activity within the nest and could clarify whether the stage-dependent patterns observed in this study are associated with changes in parental behaviour or developing offspring. Greater species-level replication would further help determine whether such patterns reflect broader nest-type differences or species-specific reproductive strategies. Moreover, having iButton sensors in the same nests at multiple points throughout a breeding attempt would be instrumental and would allow thermal conditions to be followed directly as nests transition through developmental stages, rather than relying primarily on comparisons among different nests sampled at different stages. Repeated monitoring across contrasting weather conditions would also better test whether the thermal consequences of nest architecture and placement become most apparent during periods of environmental stress. Differences that are subtle under typical conditions may become considerably more important during intense solar radiation, unusually high ambient temperatures, prolonged rainfall, or combinations of high temperature and humidity. The absence of strong structural differences under the conditions sampled in this study therefore does not preclude a thermoregulatory role for nest architecture or placement under more extreme conditions.

Ultimately, future research would benefit from integrating the microclimate and nesting-success components examined separately in this study. Simultaneously measuring environmental exposure, internal nest conditions, parental behaviour, predator activity, and reproductive outcome would make it possible to evaluate whether particular thermal environments confer measurable reproductive advantages or costs. This is especially important because the nest characteristics that improve thermal regulation may not be the same characteristics that reduce predation risk. An integrated approach could therefore evaluate whether thermal protection, concealment, predator accessibility, and other components of reproductive performance impose competing ecological pressures, rather than assuming that conditions favourable for one function are necessarily favourable for another. Such an approach would provide a more complete understanding of how nest architecture, placement, thermal conditions, and predation interact to shape reproductive outcomes in Grenada's resident landbirds.

5.4 Management Recommendations

Grenada's landscapes have already undergone substantial alteration, and the conservation of remaining natural habitats will be critical to ensuring the long-term persistence of its resident landbird communities. This study shows that nesting success is shaped by a combination of nest structure, placement, and exposure to a diverse predator community. As such, effective conservation strategies must account for these interacting factors, rather than focusing on single drivers in isolation.

Predation from both invasive ground predators and native arboreal predators indicates that nests are vulnerable across multiple vertical strata. This suggests that management actions targeting only one predator group are unlikely to be effective. Instead, invasive predator control should be implemented within a coordinated, system-specific framework that recognizes potential interactions among predator populations and the broader food web. For example, removing larger predators without considering these interactions may lead to unintended consequences, such as increases in black and brown rat populations in Grenada, consistent with the mesopredator release hypothesis (Courchamp et al., 1999). This ecological cascade occurred on Little Barrier Island, New Zealand, where managers eradicated cats as a management tactic. However, this triggered a rapid increase in invasive Pacific rat (*Rattus exulans*) populations, which were no longer being kept in check. That eradication event severely reduced nesting success for resident seabirds (Rayner et al., 2007). Therefore, targeting mongoose or feral cat populations in Grenada without a simultaneous, sustained strategy to suppress invasive rats risks exacerbating overall nest failure rates.

Partnerships with local stakeholders, landowners, and conservation organizations are particularly important and should form a central component of these management efforts. Existing Grenadian organizations already provide important foundations upon which future conservation initiatives can build. The Gaea Conservation Network, for example, has conducted training and practical capacity-building activities related to invasive-predator monitoring and control, including mongoose and rodent management. They also have community-led habitat restoration projects and integrate local communities through structured citizen science initiatives. Belmont Estate similarly demonstrates how privately managed agricultural landscapes can

contribute to bird conservation through environmental education, research partnerships, biodiversity-conscious land management, and the maintenance within a working agroecosystem. Strengthening collaborations among researchers, conservation organizations, landowners, and local communities could therefore improve both the ecological relevance and long-term continuity of conservation actions. Meaningful involvement of local residents is particularly important because communities possess locally grounded ecological knowledge and practical experience that may provide insights not readily captured through short-term research programs. Local participation can also strengthen ownership of conservation initiatives and improve their continuity beyond the duration of externally funded research or management projects. Rather than relying solely on externally designed interventions, conservation programs should therefore prioritize capacity building, knowledge exchange, and sustained partnerships with organizations and communities already engaged in the stewardship of Grenada's landscapes.

Nesting birds' use of both natural and anthropogenic substrates further highlights the importance of maintaining a heterogeneous habitat mosaic. In a highly modified system such as Grenada, conservation efforts should extend beyond protected forest areas to include agroforestry systems, gardens, and developed landscapes that continue to support nesting activity. Management within these environments should aim to retain structural diversity, including suitable vegetation, nesting substrates, and a range of nesting heights, rather than promoting overly simplified habitat conditions. This aligns with previous research on Grenadian landbirds and emphasizes the ecological value of human-modified environments when they retain sufficient habitat complexity to support breeding birds (Williams et al., 2023).

Overall, findings suggest that conservation of Grenada's landbirds will require integrated, multi-scale approaches that consider predator dynamics, habitat structure, and species-specific nesting strategies. Variation in the costs and benefits associated with different nesting strategies across habitat conditions, predator communities, and other environmental pressures means that no single management action will be equally appropriate for all species or nesting strategies. Adaptive, site-specific approaches that incorporate continued monitoring will therefore be important for supporting reproductive success and maintaining the long-term persistence of Grenada's resident landbird communities.

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Chapter 6: Conclusion

This study addressed an important gap in the literature by examining how nest architecture and nest-site characteristics influence nesting success in Grenada, as well as whether open-cup and enclosed nests differ in the microclimatic conditions they provide to resident landbirds. The study encompassed 11 commonly occurring landbird species across two field components conducted in 2023 and 2025.

The 2023 nesting-success component demonstrated that reproductive outcomes were shaped by context-dependent relationships among nest architecture, nest placement, microhabitat, and broader site conditions. Open-cup nests exhibited higher daily survival rates and cumulative survival probabilities than enclosed nests, while survival increased more strongly with nest height among open-cup nests than among enclosed nests.

Microhabitat characteristics further influenced nesting outcomes, although their effects were context-dependent. Contrary to expectations, the data suggest that increased canopy density was associated with reduced survival among open-cup nests, potentially reflecting greater predator concealment or accessibility rather than improved nest concealment. Additionally, Site-level differences in survival further indicate that reproductive success was influenced by broader habitat context beyond the immediate nest site, potentially including differences in vegetation structure, disturbance, and local predator communities. The 2023 nesting success findings suggest that the consequences of nest architecture depend partly on where nests are positioned

rather than reflecting the protective value of nest structure alone. Importantly, the observed differences between open-cup and enclosed nests may reflect broader suites of nesting strategies associated with each nest type rather than the isolated effect of nest architecture itself.

As a secondary objective, the 2025 field component expanded this work by examining how nest microclimate differed between nest types and breeding stages, and how associated microhabitat characteristics influenced these thermal conditions. Overall, internal nest temperatures closely tracked ambient conditions, with little evidence that open-cup and enclosed nests differed consistently in their thermal response across the daily cycle. Nest height and canopy density likewise did not significantly influence thermal offset. Although differences between nest architectures were not statistically significant within reproductive stages, descriptive patterns varied across the breeding cycle, suggesting that the thermal consequences of nest architecture may depend partly on reproductive stage and the biological activity occurring within the nest.

Taken together, these results suggest that nest microclimate in Grenada is not readily explained by nest architecture, reproductive stage, or measured microhabitat characteristics alone, but instead reflects multiple interacting influences, including physical nest structure, biological activity within the nest, and surrounding environmental conditions. Importantly, interpretation is constrained by the limited number of independent nests and short monitoring periods, which reduce the precision of population-level inference. Nevertheless, these findings

provide valuable baseline information on the thermal ecology of Grenada's resident landbirds and identify important avenues for future investigation.

Importantly, the nesting-success and microclimate components of this study were not designed to test whether nest thermal conditions directly influenced reproductive success. Therefore, no causal relationship between the thermal patterns documented in 2025 and the nesting outcomes observed in 2023 can be inferred from the present study. Nevertheless, considering the two components together highlights a broader question concerning how different ecological pressures interact to shape nesting strategies. A nest site that reduces exposure to predators may not necessarily provide the most favourable thermal conditions, and characteristics that improve concealment or physical protection may carry different costs and benefits depending on reproductive stage, predator community, and environmental conditions.

Both phases of this study provide complementary insight into the reproductive ecology and thermal environments experienced by Grenada's resident landbirds and demonstrate that the ecological consequences of nest architecture are strongly dependent on the context in which nests occur. More broadly, the findings illustrate the that fundamental components of avian reproductive ecology emerge from interconnected ecological trade-offs instead of single, isolated mechanisms. This context dependence may become increasingly important as Caribbean ecosystems experience continued climatic and anthropogenic change, because shifts in

temperature, habitat structure, disturbance, and predator communities may alter both the costs and benefits associated with different nesting strategies. Understanding how these pressures interact will therefore be important for identifying species or nesting strategies that may be particularly vulnerable and for anticipating how Grenada's resident landbird community may respond to novel or intensifying environmental pressures. By integrating nest architecture, nest-site selection, predator dynamics, microclimate, and reproductive performance, future research can build upon the baselines established here to determine how these interacting forces ultimately shape avian fitness and population persistence in a changing Caribbean environment.