

Ecology and conservation of the Sali (Micronesian Starling, *Aplonis opaca*)
in the presence of the invasive Brown Treesnake (*Boiga irregularis*)
in Guam, Mariana Islands

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ABSTRACT

The world's islands are of singular importance from a conservation perspective because they hold a disproportionate share of global biodiversity. However, island ecosystems are fragile, and the introduction of invasive species poses an especially grave threat to their species. My research took place on the island of Guam, which has been particularly hard hit by invasive species in recent history. The introduction of the invasive Brown Treesnake (BTS; *Boiga irregularis*) to Guam in the mid-20th century caused the extinction of the vast majority of its avifauna. Of the remaining bird species, the native Sâli (*Aplonis opaca*) is a forest starling now limited to breeding and roosting in certain urbanized areas on the island. Previous research has shown that although Sâli adults appear to have high survival, their fledglings are highly vulnerable to predators. My research focused on refining our understanding of how BTS are impacting Sâli ecology and survival, and how BTS management can benefit Sâli conservation. In my first chapter, I conducted the first field study to investigate the influence of both prey and predator sizes on the frequency of ingestion success by snakes. I found that nearly half of ingestion attempts by BTS on fledgling Sâli were unsuccessful, and that BTS routinely pushed the upper limits of their capacity to swallow prey. These results suggest that relatively small BTS pose a greater predation risk to birds than previously recognized, and broaden the size range of BTS that should be targeted in management efforts for avian conservation. In my second chapter, I investigated a potential life-history trade-off for Sâli between the proximity of nest sites to foraging areas and the risk of fledgling predation by BTS. I found that Sâli nesting closer to the forest make more yearly nesting attempts, but that fledgling survival was higher the farther their nest site was from the forest. Sâli therefore balance potential fecundity with predation risk to fledglings in their selection of nest sites. In my third chapter, I examined the survival response of fledgling Sâli to the suppression of BTS. I found that snake control did not lead to a change in

fledgling survival from the pre-treatment baseline or in comparison to areas where snakes were not controlled, and that there was no shift from snake predation to other causes of mortality. Changes to the strategies or tools employed will therefore be required in order for future BTS control efforts within similar habitats to effectively improve avian survival. This body of work demonstrates that BTS are affecting Sli in unexpected ways, and offers new guidance on how to manage damaging invasive species for native species conservation.

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GENERAL AUDIENCE ABSTRACT

Islands are of high value important for conservation because they hold a more than their share of the world's animal and plant species. However, island ecosystems are fragile, and the introduction of damaging exotic species is especially threatening to species that live there. My research took place on the island of Guam, which has been particularly hard hit by damaging non-native species in recent history. The introduction of the Brown Treesnake (BTS; *Boiga irregularis*) to Guam in the mid-20th century caused the extinction of the vast majority of its bird species. Of the remaining bird species, the native Sâli (*Aplonis opaca*) is now limited to breeding and roosting in certain developed areas on the island. Previous research has shown that although Sâli adults appear to have high survival, their fledglings (young birds that recently left the nest) are highly vulnerable to predators. My research focused on refining our understanding of how BTS are impacting Sâli life cycles, and how BTS management can benefit Sâli conservation. In my first chapter, I conducted the first field study to investigate the influence of both prey and predator sizes on the capacity for snakes to swallow their prey. I found that nearly half of attempts by BTS to swallow fledgling Sâli were unsuccessful, and that BTS routinely pushed the upper limits of their capacity to swallow prey. These results suggest that relatively small BTS pose a greater predation risk to birds than previously recognized, and broaden the size range of BTS that should be targeted in management efforts for avian conservation. In my second chapter, I investigated a potential life-history trade-off for Sâli between how close their nest sites are to foraging areas and the risk of fledglings being killed by BTS. I found that Sâli nesting closer to the forest make more nesting attempts per year, but that fledgling survival was higher the farther their nest site was from the forest. Sâli therefore balance the potential number of young they can raise with the predation risk to those same young in their choice of nest sites. In my third chapter, I examined whether the suppression of BTS led to a change in the survival

of fledgling Såli. I found that snake control did not lead to a change in fledgling survival from the period before the treatment or in comparison to areas where snakes were not controlled, and that there was no shift from snake predation to other causes of death. Changes to the strategies or tools employed will therefore be required in order for future BTS control efforts within similar habitats to effectively improve avian survival. This body of work demonstrates that BTS are affecting Såli in unexpected ways, and offers new guidance on how to manage damaging invasive species for native species conservation.

*For Nora,
who grew up alongside
this dissertation*

*and Melissa,
without whom none of this
would have been possible.*

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Haldre Rogers has been the constant throughout, and I could not have asked for a better supervisor. She has pushed me to ground my research in theory, ask bigger and better questions, and take exponential leaps as a quantitative ecologist. She gave me, as with all her students, a long enough leash to lead many aspects of the research, while always providing enough guidance to keep things on track. She balances discipline, rigour and ambition with a unique bright-eyed curiosity that invariably leads to positive outcomes for all projects she is involved with. Besides her role as an advisor, Haldre is a good friend that I've had the fortune of sharing many a hike, ultimate frisbee game, tasty meal and craft beer with. My labmates at Iowa State, Virginia Tech and University of Missouri–St Louis have provided fantastic companionship, both virtual and in person, and I expect that we will remain friends and continue to collaborate for many years to come.

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As a Canadian living and working on Guam, who transferred from Iowa State University to Virginia Tech midway through his doctorate, I have been the source of countless headaches to administrators, and could never have completed my journey through graduate school without their tireless help. Among many others, I am particularly grateful for the help of Jennifer Phillips, Matt Grice and Joel Snodgrass (Fish and Wildlife Conservation department chair) at Virginia Tech.

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The people of Guam have experienced, and continue to feel, the devastating effects of centuries of colonial occupation. My research took place on military lands which were seized from landholding families during wartime and never returned to their rightful owners, in many cases without subsequent reparation. It is crucial that these injustices, along with the countless other harms of colonialism and militarism, are neither forgotten nor normalized.

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Attributions

Chapter 1 (published)

Martin Kastner: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Scott M. Goetz:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); writing – review and editing (supporting). **Kayla M. Baker:** Investigation (equal); writing – review and editing (supporting). **Shane R. Siers:** Writing – review and editing (supporting). **Eben H. Paxton:** Writing – review and editing (supporting). **Melia G. Nafus:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); writing – review and editing (supporting). **Haldre S. Rogers:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (equal); writing – review and editing (supporting).

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Table of Contents

Abstract.....	ii
General audience abstract	Error! Bookmark not defined.
Acknowledgements.....	vii
Attributions	x
Table of Contents.....	xi
Introduction.....	1
1.1 Research context and objectives	1
1.2 Study site.....	2
1.3. Study species.....	3
1.3.1 Prey species.....	3
1.3.2 Predator species.....	3
1.4 Bibliography.....	5
CHAPTER 1: Gape-limited invasive predator frequently kills avian prey that are too large to swallow	10
2.1 Abstract.....	11
2.2 Introduction.....	13
2.3 Materials and methods	16
2.3.1 Study site and species	16
2.3.2 Fledgling survival monitoring.....	18
2.3.3 Brown treesnake visual searches.....	20
2.3.4 Statistical analyses	20
2.4 Results.....	22
2.5 Discussion.....	23
2.6 Bibliography.....	28
2.7 Figures.....	37
CHAPTER 2: Invasive snake drives trade-off in nest site selection for an island passerine	41
3.1 Abstract.....	42
3.2 Introduction.....	43
3.3 Materials and methods	46
3.3.1 Study site and species	46
3.3.2 Nest and fledgling survival monitoring.....	47
3.3.3 Statistical analyses	48

3.4 Results.....	50
3.5 Discussion.....	52
3.6 Bibliography.....	57
3.7 Figures.....	65
3.8 Tables.....	69
CHAPTER 3: Survival of avian prey following control of an invasive ectothermic predator	76
4.1 Abstract.....	77
4.2 Introduction.....	78
4.3 Materials and methods	81
4.3.1 Study site and species	81
4.3.2 Predator control.....	82
4.3.3 Fledgling survival monitoring.....	84
4.3.4 Brown treesnake visual searches.....	85
4.3.5 Statistical analyses	86
4.4 Results.....	88
4.4.1 Predator control.....	89
4.4.2 Fledgling survival	89
4.4.3 Cause of death.....	90
4.5 Discussion	90
4.6 Bibliography.....	95
4.7 Figures.....	104
4.8 Tables.....	108
Conclusions.....	110

Introduction

1.1 Research context and objectives

Oceanic islands are disproportionately valuable for the conservation of global biodiversity due to their high concentration of endemic species. For example, although islands represent only 5.3% of the world's terrestrial surface area, they contain 19% of the world's known bird species (Tershy et al. 2015).

Conversely, islands have also been particularly hard hit by anthropogenically-driven global change, including habitat loss to development, the effects of invasive species and sea level rise (Russell & Kueffer 2019). For example, over 90% of historic avian extinctions have been on islands (Wood et al. 2017), and up to 2000 species of birds have been lost from Pacific islands alone (Steadman 1995). Invasive vertebrate predators are the leading cause of extinction of island birds, and they remain an ongoing threat to island bird species worldwide (Bellard et al. 2016).

Limited geographical ranges and small population sizes may inherently predispose island birds to an elevated extinction risk, for example due to stochastic effects. However, there are other traits of island birds, such as low fecundity and a lack of anti-predator adaptations, which exacerbate their vulnerability to invasive predators (Duncan & Blackburn 2004). As such, the removal of invasive predators is expected to be of great conservation benefit to island birds, by allowing increased survival and recruitment of extant populations, and engendering the opportunity to reintroduce extirpated species. Indeed, invasive species eradication can trigger the dramatic recovery of island bird populations (Jones et al. 2016), as well as broader ecological restoration via direct and indirect effects (Prior et al. 2018). If invasive species eradication is impossible, then ongoing control may also allow recovery of native bird species (Moorhouse et al. 2003, Vanderwerf et al. 2023). Optimizing invasive species control requires a detailed knowledge of the interactions between native and invasive species.

The overarching objective of my dissertation work is to improve our understanding of how invasive predators are impacting the survival and ecology of native birds on islands, in order to inform their

management. Three major questions underlie this objective, which will form the basis of my dissertation chapters:

1. What features of predator and prey species influence predation success?
2. How does risk of predation influence prey recruitment?
3. How does predator control influence prey survival?

1.2 Study site

The island of Guam is well suited as the focal point of a study focused on the interactions between native avian prey and invasive predators. Until the mid-twentieth century, Guam suffered losses in avian diversity typical of many tropical oceanic islands (Steadman 2006). Human colonization of Guam occurred circa 3500-4000 years before present, with Guam thought to be the first island in the western Pacific permanently inhabited by indigenous peoples (Pugach et al. 2021). Although subfossil remains indicate that several avian species were lost to extinction, it is believed that the effects of early human settlement on Guam were not as severe as they might have been otherwise because *Rattus* species were not introduced to the island until ~1000 years before present, and pigs did not arrive until European colonization (Pregill & Steadman 2009). Indeed, early European visitors marvelled at the island's lush forests containing "numberless birds" (Crozet 2011). However, in the aftermath of World War II, Brown Treesnakes were accidentally introduced to the island in cargo from the Admiralty Archipelago near Papua New Guinea (Richmond et al. 2015). Following their establishment and spread, 10 out of 12 remaining native forest bird species were extirpated, and declines or extirpations were recorded among the majority of bird species in other habitats (Savidge 1987, Wiles et al. 2003). Indirect impacts of the loss of Guam's avifauna have been severe, with drastic changes to pollination, insectivory and seed dispersal services (Mortensen et al. 2008, Rogers et al. 2012, 2017). Guam's remaining native forest birds, the Yáyaguak (Mariana Swiftlet, *Aerodramus bartschi*) and the Sáli (Micronesian Starling, *Aplonis*

opaca), are restricted to small portions of their former range, and both species continue to be heavily impacted by BTS predation (Wiles et al. 2003).

1.3. Study species

1.3.1 Prey species

Såli are medium-sized (~80-85g) passerine birds in the starling family (Sturnidae) endemic to the Mariana and Caroline Islands in Micronesia (Baker 1951). Although Såli are abundant across their range, they are locally endangered on Guam as a result of BTS predation, with a remnant population of around 1,500 individuals that largely breed and roost in the urbanized portions of a military base in northern Guam (Pollock et al. 2022). Såli are year-round cavity nesters, and on Guam, they largely breed in artificial nest structures such as streetlamp posts, metal typhoon shutters and predator-resistant nest boxes (Savidge et al. 2022). While most Såli nest sites are relatively safe from predation due to their inaccessibility to BTS, fledglings suffer exceptionally high mortality rates, primarily due to BTS and cats (~75-95%; Wagner et al. 2018, Pollock et al. 2019).

1.3.2 Predator species

BTS are nocturnal, primarily arboreal, rear-fanged snakes, with a native range spanning northern Australia, New Guinea and some Melanesian islands, and a non-native range restricted to Guam and some of its offshore islands (Rodda et al. 1999, Rodda and Savidge 2007). On Guam, BTS inhabit all terrestrial habitats, with large individuals particularly common in urbanized areas where prey are more abundant (Savidge 1991, Siers et al. 2017). They exhibit an ontogenetic dietary shift whereby juveniles feed almost exclusively on small lizards, but their diet expands to include larger endothermic prey such as birds and mammals as they attain sexual maturity (Savidge 1988, Savidge et al. 2007).

1.3.3 History of BTS management

Along with the realization in the mid-1980s that BTS were capable of causing widespread avian extirpations and extinctions, along with severe economic disruption through (most notably) their effects on power infrastructure, arose a concern that they could spread to other islands within Oceania and beyond (Rodda et al. 1999). The management of BTS therefore materialized in the early 1990s as an interdiction program with the objective of preventing any further spread of the species from Guam (Hall 1996, Engeman & Vice 2001). Management efforts were primarily implemented around air- and seaports, and were conceptually designed as a series of progressively finer filters, such that the probability of a BTS passing through the final filter is vanishingly small (Clark et al. 2018). Pragmatically, the tools deployed consisted of perimeter trapping, spotlight searches along fencelines, habitat modification around cargo-staging areas, physical barriers, and detector dog searches of cargo (Hall 1996, Clark et al. 2018).

BTS management tools are expensive and labor-intensive, and therefore research and development efforts have focused on finding more cost-effective and scalable tools. In the early 2000s, researchers discovered that the human pharmaceutical acetaminophen is a deadly toxicant to BTS (Johnston et al. 2002, Clark et al. 2012). Toxic baiting has been progressively integrated into control networks, with the toxicant delivered to BTS via carrion bait (Clark et al. 2012, Clark et al. 2018). While toxic bait is generally deployed in bait stations, an aerial delivery system has been developed that has the capacity to rapidly saturate large areas with bait (Lardner et al. 2013, Siers et al. 2019). Other alternative management tools, such as synthetic baits, pheromone attractants, and the use of fumigants, have been investigated but have yet to move into practical application (Clark et al. 2018).

Although the bulk of BTS management remains focused on interdiction efforts, there has been an increasing focus on implementing BTS control for native species conservation and restoration. For example, tentative efforts have been made to control BTS around Yáyaguak caves in southern Guam (Klug et al. 2021). The aerial delivery of toxic bait could, in principle, allow the suppression of BTS over large areas of forest and benefit the recovery of native species (Siers et al. 2020). Modeling and planning

tools offer greater clarity on the level of BTS suppression needed to enable recovery of native bird species, and on the geographic areas where restoring ecosystem services may be most beneficial (Thierry & Rogers 2020, McElderry et al. 2022). Chapter 3 describes the results of a control effort implemented within the remnant roosting and breeding habitat of native Sali.

The discovery in 2020 of an incipient BTS population on Islan Dano'/Cocos Island, an offshore island south of Guam with significant conservation value, has mobilized BTS management efforts for conservation at a scale not yet seen on mainland Guam (Barnhart et al. 2022). Standard BTS control tools (traps and toxic bait) were not effective at removing BTS from the island, perhaps due to an abundance of alternative prey (Siers et al. 2024). In contrast, visual searches have proven relatively effective (Siers et al. 2024). A volunteer-run effort mobilized to conduct BTS searches on Islan Dano', providing the first opportunity for community involvement in BTS control and a cost-effective alternative to BTS management conducted by government agencies (Kastner & Terral 2023).

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CHAPTER 1:

Gape-limited invasive predator frequently kills avian prey that are too large to swallow

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2.1 Abstract

Gape-limited predators (e.g., snakes, many fish) are not generally expected to pose a predation threat to prey that are too large for them to swallow. However, the extent to which snakes predate on prey that exceed their gape limitation remains largely unknown. We conducted the first study to investigate the influence of both prey and predator sizes on the frequency of ingestion success by snakes in a natural system. We combined survival monitoring of an avian prey species (*Aplonis opaca*) via radio-telemetry with a survey of the size distribution of their major predator (*Boiga irregularis*) on Guam. This allowed us to assess (1) the frequency of unsuccessful ingestion by the predator, (2) whether the size of prey predicts ingestion success, (3) whether the size of the predator predicts ingestion success, and (4) the relationship between prey and predator sizes in successful ingestion attempts. We found that nearly half (47.95%) of ingestion attempts by snakes on fledgling birds were unsuccessful, and no instances where unsuccessful ingestion caused the mortality of the snake. Attempts to consume smaller fledglings were as likely to be unsuccessful as attempts to swallow larger fledglings. However, snakes that successfully ingested fledglings were among the largest snakes in the population, and larger than average conspecifics attracted to endothermic prey. The smallest snakes that successfully ingested fledglings attained remarkably high relative prey mass values for their species, consuming prey weighing up to 79.9% of their own mass. Our study indicates that *B. irregularis* routinely predate prey that are too large for them to successfully ingest, which causes mortality to the prey but poses little risk to the predator. The potential reward for snakes in consuming oversized prey may outweigh the inherent risks, while instances of predation that do not result in consumption may have considerable impacts on prey populations.

2.2 Introduction

Predation attempts have the potential to shape the abundance, demographic structure and behaviour of prey populations via both indirect and direct pathways. Broadly, unsuccessful predation attempts are expected to compose the majority of predator-prey interactions, although success rates are highly variable across predator taxa (Vermeij, 1982). For example, most studies of raptorial birds have documented post-detection predation success rates lower than 20%, while predation efficiency approaching 100% has been reported for crabs, fish and other taxa, albeit on the most vulnerable life stages of their prey (Abrams, 1989; Vermeij, 1982). Numerous factors relating to prey influence predation success, including behavioural factors like habitat selection (Sih, 1985), evasive behaviours (Christensen, 1996), and learned recognition of predator cues (Acquistapace, Hazlett & Gherardi, 2003), as well as physical factors including crypsis (Ruxton et al., 2019), group size and composition (De Luna et al., 2010), health status (Semlitsch, 1990), mechanical defense (Sawyer et al., 2009), and, crucially, the size of prey relative to predators (Weitz & Levin, 2006).

Predators that increase in size as they mature generally broaden their diet by gradually increasing the maximum size of their prey (Christensen, 1996; Vézina, 1985). Indeed, optimal foraging theory predicts that predators should select prey that provide the highest energy return per unit of handling time (Stephens & Krebs, 1986). Conversely, an increase in prey body size relative to the size of a given predator has been shown to greatly reduce predation risk, due either to a reduction in capture or handling efficiency by the predator or their more rapid satiation (Semlitsch, 1990). For example, in New Zealand, juvenile North Island Brown Kiwi (*Apteryx mantelli*) suffer intense predation by invasive stoats (*Mustela erminea*) for their first months of life until they attain a size refuge, beyond which they are no longer vulnerable to stoat predation (McLennan et al., 2004). For gape-limited predators, such as many fish, lizards, and birds, and most snakes, the upper threshold in prey size is predicted to be dependent on the relationship between the size of the predator's mouth and the widest point of the prey item. The individual-level risk of predation by a gape-limited predator is expected to drop abruptly once the widest

point of the prey's body exceeds a corresponding measure of the predator's mouth size (Christensen, 1996). However, the degree to which individual predators are capable of judging their own gape size and the consequences of attempting to ingest prey that are too large to swallow are relatively poorly characterized.

Snakes are an almost universally gape-limited clade that have evolved a variety of behavioural, physiological, and mechanical strategies that enable them to consume larger prey items (i.e., heavier and/or bulkier, *sensu* Greene & Wiseman, 2023). Snakes serve as a model system for studying how the relative size of predators and prey affects diet and feeding ecology (Greene, 1983; Jayne et al. 2022). Body size in many snake species is positively correlated with the maximum size of their prey (Arnold, 1993; King, 2002; Shine, 1991). However, data on the success of predation attempts in snakes, and its relationship to prey size, remain scarce because of the cryptic nature of many species. Data on snake diet are generally based on gut contents of museum specimens, or prey items that are forcibly regurgitated by free-ranging snakes, thus only recording successful ingestion events but not reflecting a comprehensive picture of predation attempts (Costa & Trevelin, 2020; Glaudas, Kearney & Alexander, 2017). Studies on snake predation success often take place in a laboratory setting, which may not be representative of natural conditions for predator or prey (Clark, 2006). Anecdotal reports of unsuccessful predation from nature indicate that success rates may be lower than previously assumed (Costa & Trevelin, 2020). Field-based empirical studies have found that the success rate of predatory strikes by ambush-hunting snakes in hitting their targets is generally around 50% or lower (e.g. Clark, 2006; Clark, Tangco & Barbour, 2012; Glaudas et al., 2017). However, for a gape-limited predator such as a snake, incapacitating a prey item is only half the battle – they must still manage to swallow it whole.

Results from the few studies that have documented the ingestion success of snakes suggest that they may regularly kill prey that are too large for them to successfully ingest. For example, Shedao Island Pit Vipers (*Gloydius shedaoensis*) are often observed capturing and attempting to feed on birds that they are unable to swallow (Shine & Sun, 2003). A recent telemetry study on koala (*Phascolarctos cinereus*)

survival found that only slightly more than a third (38%) of the koalas killed by carpet pythons (*Morelia spilota*) were successfully ingested by the snakes (Robbins et al., 2019). There are also many anecdotal reports of snakes attempting to ingest oversized prey (Kornilev, Natchev & Lillywhite, 2023). These reports raise the questions of how frequently snakes are unsuccessful in consuming captured prey, and how ingestion success relates to the relative sizes of prey and predators. Aside from energetic, time, and, in some cases, venom costs, snakes also incur a risk of injury or death when attempting to consume oversized prey (Kornilev et al., 2023). There are therefore competing hypotheses as to why snakes may attempt to ingest such prey: these attempts may either be dangerous mistakes triggered by visual or chemical cues, or alternatively, they are calculated risks where the potential benefits outweigh the likely harm. Sazima and Martins (1990) speculate that predation attempts on oversized prey may be especially prevalent in young snakes, perhaps due to inexperience, or the unavailability of appropriately sized prey. However, Feder and Arnold (1982) predicted that it would be beneficial for snakes to attack large or difficult prey, even if such prey are ingested only occasionally, because of the potential for a substantial energetic reward. This implies that snakes may regularly attempt, but fail, to ingest prey that are too large for them to swallow. To our knowledge, no study to date has investigated the influence of both prey and predator sizes on the frequency of ingestion success in a natural system.

The island of Guam (indigenous CHamoru name: Guåhan), in the tropical western Pacific, offers a unique opportunity to conduct a detailed field study on the ingestion success of snakes. Brown Treesnakes (*Boiga irregularis*, BTS) became established on Guam after their accidental introduction following World War II, and subsequently spread across the island causing the local or total extinction of most native forest bird species (Savidge, 1987). BTS are a relatively large colubrid snake species, attaining a maximal length of over 3 m and weighing up to 200 times more as adults than as neonates (Jayne et al., 2022; Rodda et al., 1999). The diet of BTS on Guam is broad, including a variety of reptile, amphibian, bird, and mammal species, which are acquired through a mix of active and ambush foraging in arboreal and terrestrial habitats (Rodda, 1992; Rodda et al., 1999; Savidge, 1988). BTS have been linked with declines

or extinctions in native prey species (Rodda & Fritts, 1992; Savidge, 1987), and indirect effects of their invasion are having ongoing and severe ecosystem-wide repercussions (Rogers et al. 2017). While endothermic prey populations have collapsed in forested areas, commensal non-native birds and mammals in urbanized areas continue to provide a relatively rich prey base for BTS (Savidge, 1991; Siers, Savidge & Reed, 2017). Certain native bird species, including the omnivorous Sâli (Micronesian Starling, *Aplonis opaca*), have also persisted and even recovered in urbanized areas, despite the ongoing threat of predation by BTS (Pollock et al. 2019, 2022; Wiles et al. 2003). Although all life stages of Sâli are subject to BTS predation, fledgling birds experience particularly high mortality rates (Pollock et al., 2019).

In this study, we used radio-telemetry to monitor the fate of fledglings from the largest remaining population of Sâli on Guam. We captured BTS that successfully consumed Sâli, and identified fledglings that were unsuccessfully ingested by BTS by their characteristic saliva-coated head and nape (Savidge, 1988; Pollock et al., 2019). We also gathered data on the overall BTS population at the site by taking morphological measurements on all individuals found during visual surveys. We focused our study on four major questions: (1) what proportion of ingestion attempts by BTS on Sâli fledglings are unsuccessful, (2) does the size of the prey predict ingestion success, (3) does the size of predator predict ingestion success, and (4) for successful ingestion attempts, what is the relative size of predators with respect to that of their prey?

2.3 Materials and methods

2.3.1 Study site and species

2.3.1.1 Study site

We conducted our study between November 2019 and October 2022 on Guam, the largest island in Micronesia and southernmost in the Mariana Islands archipelago. Guam experiences a tropical climate

with a dry season from January to June and a wet season from July to December. We studied interactions between Sâli and their major predator, BTS, on Andersen Air Force Base (AAFB), an 8,100 ha military installation on the northern tip of the island. Specifically, we focused on the Sâli breeding range, which spans roughly 500 ha in the urbanized southeastern portion of AAFB. This area is characterized by residential, commercial, and administrative buildings within expansive areas of lawn and isolated ornamental trees, bordered by native limestone forest to the east and mixed introduced forest interspersed with residential areas to the south. BTS control, primarily using poison bait and traps, was ongoing over some portions of the site during our study.

2.3.1.2 Prey species

Sâli are medium-sized passerine birds (75 g upon fledging, 85 g as adults) in the starling family (Sturnidae) endemic to the Mariana and Caroline Islands (Baker, 1951). Although Sâli are abundant across their range, they are locally endangered on Guam as a result of BTS predation, with a remnant population of around 1,500 individuals that largely breed and roost within our study site (Pollock et al., 2022). Sâli are year-round cavity nesters, and on Guam, they mostly breed in artificial nest structures such as streetlamp posts, metal typhoon shutters, and nest boxes (Savidge et al., 2022). While Sâli nest sites on AAFB are generally relatively safe from predation, fledglings suffer exceptionally high mortality rates in the first weeks after they leave the nest, primarily due to BTS and cats (~75-95%; Pollock et al., 2019; Savidge et al., 2022).

2.3.1.3 Predator species

BTS are nocturnal, primarily arboreal, rear-fanged snakes, with a native range spanning northern Australia, New Guinea and some Melanesian islands, and a non-native range restricted to Guam and some of its offshore islands (Rodda et al., 1999; Barnhart et al., 2022). On Guam, BTS inhabit all terrestrial habitats, with large individuals particularly common in urbanized areas where prey are more abundant (Savidge, 1991; Siers et al., 2017). BTS on Guam smaller than 700 mm snout-vent length (SVL) are

classified as juveniles, and those larger than 1025 (females) or 1030 (males) mm SVL as mature, while individuals between those size classes are considered to be in a transitional phase (Siers et al., 2017).

They exhibit an ontogenetic dietary shift whereby juveniles feed almost exclusively on small lizards, but their diet expands to include larger endothermic prey such as birds and mammals as they enter the transitional phase (Savidge, 1988; Lardner et al., 2009). The size at which this shift occurs is variable; BTS as small as 650 mm SVL have eaten birds in captivity (Savidge, 1988), and the smallest snake in the wild on Guam to have been documented consuming avian prey measured 717 mm SVL (S. Siers, USDA, written communication, 2023). BTS larger than 900 mm SVL are consistently attracted to endothermic prey (Rodda et al., 2007), and, in urbanized habitats, the proportion of birds and mammals in their diet expands rapidly while the proportion of lizards declines to zero (Savidge, 1988; Siers, 2015). Avian populations on Guam appear to be particularly sensitive to the presence of BTS larger than 900 mm SVL (Nafus et al., 2024).

2.3.2 Fledgling survival monitoring

The Sâli fledglings in our study hatched from an array of predator-proof nest boxes ($n = 70$) installed across urbanized areas of AAFB (Savidge et al., 2022). Nestlings were banded at 22-23 days post-hatching with a size 2 or 3 U.S. Geological Survey (USGS) metal band and a unique combination of three Darvic colour bands to allow individual identification. At the majority of nests (72%), we also attached a radio-transmitter (BD-2, battery life ~175 days, Holohil Systems Ltd., Carp, Ontario, Canada; or PowerTag, battery life ~46 days, Cellular Tracking Technologies, Rio Grande, New Jersey, USA) to one or more nestlings per brood with a modified leg-loop harness (Rappole & Tipton, 1991). Both transmitter types had a pulse rate of one pulse per 3 seconds. To avoid any deleterious effects, we ensured that the combined mass of the bands, harness, and transmitter weighed less than 4% of the nestling's body mass (Barron, Brawn & Weatherhead, 2010).

We conducted survival checks on Sâli fledglings using hand-held radio-telemetry receivers. Fledglings were checked daily for the first 15 days post-fledging, when mortality is highest (Pollock et al., 2019), then three times per week from 16 to 30 days post-fledging, and at least once per week from 31 days post-fledging and beyond, until the transmitter stopped functioning due to depleted batteries. We obtained visual resights of fledglings and confirmed their identity using their unique colour-band combinations. The transmitter signal can still be picked up when it is inside a snake, so we were able to capture snakes after they successfully consumed a tagged fledgling.

When we encountered a dead radio-tagged fledgling, we assigned cause of mortality as (1) successfully ingested by BTS if it was found inside a snake, or its transmitter had been gut-passed by a snake (fecal matter found on the transmitter), (2) unsuccessful ingestion attempt by BTS (informally referred to as “slimed”) if the fledgling had characteristic saliva-matted feathers on its head and body (Figure 1; Savidge, 1988; Pollock et al., 2019), (3) cat predation, if it had been partially or fully consumed with feathers, wings and/or feet remaining, often accompanied by a broken transmitter harness, and (4) unknown, if it was found without signs of predation and without conclusive evidence indicating cause of mortality. Other causes of mortality (e.g. starvation, entanglement) were assigned as they were encountered, based on available evidence. No predator species on Guam other than BTS would leave a saliva coating over birds’ heads and bodies due to failed ingestion attempts or other handling.

When possible, we hand-captured BTS that had consumed radio-tagged fledglings during daily survival checks. When they were in inaccessible refugia (e.g., a small cavity), we returned nightly between four and six nights post-consumption, when BTS re-emerge following a period of reduced activity during digestion (Siers, Yackel Adams & Reed, 2018). Once captured, BTS were transferred to the Guam National Wildlife Refuge, where they were housed in a climate-controlled room, in 5-gallon buckets with water dishes and air vents, until they completed digestion and passed the Sâli remains and transmitter. We then recorded morphometrics for the snake following the procedures described below, after which they

were released at their point of capture. We were unable to capture the snake on 33 occasions, in which case we recovered the transmitter after gut passage to definitively confirm the fledgling's cause of death.

2.3.3 Brown treesnake visual searches

We surveyed the BTS population at our study site between December 2019 and November 2022 to characterize the size distribution of snakes on the landscape. To do so, trained observers visually searched individual trees using high-powered headlamps. We searched individual trees for a set amount of time that varied between 0:15 and 3:00 minutes depending on the structural complexity of the tree species. We included all snakes incidentally observed on the ground between directed searches of trees. We attempted to capture all observed snakes, and upon capture collected morphological data including SVL (mm), weight (g), and sex. Prior to release, we uniquely marked all snakes not previously captured with a subcutaneously injected passive integrated transponder and ventral scale clips, which allowed us to determine if the same snake successfully consumed multiple fledglings in our study.

Visual searching is the only known survey method to successfully sample all size classes of BTS (Rodda et al. 2007). However, results from a capture-mark-recapture study in forested habitat indicate that detection probabilities vary across BTS size classes, and visual searches may under-represent the smallest and largest size classes (Christy et al., 2010). Because the smallest BTS size class is not attracted to endothermic prey (and thus irrelevant to our analysis), and large BTS are generally scarce, we do not believe that a bias towards mid-sized snakes is likely to substantively affect our results. Nevertheless, we caution that our resulting size distribution (Figure 3) should not be taken as a perfect reflection of relative BTS abundances across size classes on the landscape. Although relative detectability by size class across habitat types has yet to be assessed, we expect that overall detectability is likely to be higher in an open, urbanized setting such as our study site, compared to a more visually complex forested environment.

2.3.4 Statistical analyses

To quantify the proportion of Sáli ingestion attempts by BTS that were unsuccessful, we calculated the proportion of Sáli that were found slimed relative to those found ingested by BTS.

To assess whether the probability of being consumed by a BTS is related to prey size, we ran a generalized linear model with a binomial distribution with fledgling fate (consumed or slimed) as the dependent variable and fledgling mass as a continuous independent variable. We examined residual plots to assess model fit and used a Wald test to assess significance.

We used a bootstrapping approach to determine whether the size of the predator predicted ingestion success. While we could use the bird's transmitter signal to track and capture snakes that successfully ingested Sáli fledglings, our methods did not allow us to locate snakes that failed to ingest birds; thus, we cannot directly compare the sizes of snakes that were successful in ingesting Sáli to those that were not. However, we hypothesized that if snake size does not influence predation success, then the size of snakes captured after successful ingestion should not differ from a random sample of snakes on the landscape that are attracted to endothermic prey. Although smaller BTS have been recorded consuming avian and mammalian prey, we set the lower size threshold for the ontogenetic shift when BTS become consistently attracted to endothermic prey at 900 mm (Rodda et al., 2007). Therefore, we compared the size distribution of snakes captured after successfully consuming Sáli to the size distribution of BTS larger than 900 mm SVL sampled in visual surveys across our study site. Because the sample of snakes that successfully consumed Sáli was only 52, compared to a sample of 265 snakes that were captured through visual surveys, we repeatedly subsampled 52 snakes from the truncated visual survey dataset. We calculated the mean size for each of these 5000 samples, which gave us a distribution of mean sizes, from which we calculated 95% confidence intervals. We then determined whether the mean size of snakes found successfully ingesting Sáli fell within the 95% confidence intervals of the distribution of mean sizes of endothermic-prey-eating snakes on the landscape.

We calculated relative prey mass for all successful predation attempts by dividing prey (Sáli fledgling) mass by the mass of its respective predator (BTS). We used a linear model with a Gaussian distribution to

test whether the mass of snakes (independent variable) is related to the mass of their prey (dependent variable). We visually inspected diagnostic plots of the residuals to assess model fit and used a Wald test to assess significance.

All analyses and graphing were performed using R Statistical Software (v4.2.2; R Core Team, 2022), including packages *boot* (Davison & Hinkley, 1997; Canty & Ripley, 2021) for the bootstrapping analysis, *ggResidpanel* (Goode & Rey, 2019) for examining model fit, and *ggplot2* (Wickham, 2016) for graphing. All values are presented as mean (μ) \pm standard error (SE) unless otherwise stated, and we accepted significance at $\alpha < 0.05$.

2.4 Results

We recorded 294 Sáli fledgling mortalities out of 461 fledglings tracked, of which 171 (58%) were attributed to BTS, and 89 (30%) to cats. Among BTS-caused mortalities, 82 fledglings (48%) were slimed but not ingested by BTS and 89 (52%) were ingested (Figure 2). Two of the slimed fledglings had been scavenged by cats, but their mucus-coated heads were present among the remains, allowing us to determine their primary cause of death. For the other mortalities attributed to cats, we were unable to differentiate between direct kills and scavenging events because there were insufficient carcass remains to allow a definitive determination.

The probability of being slimed or consumed by BTS did not depend on fledgling mass ($z = -0.515$, $p = 0.890$), which had a mean of $73.3 \text{ g} \pm 0.7$, and a range of 60.5 to 86.3 g.

We captured 52 individual snakes that consumed Sáli (55 total capture events, i.e., 3 individuals captured twice; 21 female, 28 male, and 3 of unknown sex), with a mean SVL of $1206 \text{ mm} \pm 23$ (range: 1023 – 1593 mm). During visual surveys, we captured 265 individual snakes (354 total capture events, i.e., 89 recaptures; 131 were female, 121 male, 10 juvenile, and 3 of unknown sex), with a mean SVL of $933 \text{ mm} \pm 15$ (range: 288 – 1989 mm). The mean SVL calculated from the means of each of our 5000

bootstrapped subsamples of 52 snakes was 1114 mm (1068 – 1165 mm 95% quantile means) for BTS over the 900-mm threshold. The mean size of BTS found successfully ingesting Sålí fell outside (above) the 95% confidence interval around the mean size of BTS larger than 900 mm SVL, indicating that snakes captured after successfully ingesting Sålí were not a random sample of snakes on the landscape attracted to endothermic prey (Figure 3).

We did not find any relationship between snake mass and the mass of Sålí fledglings they consumed ($t = -0.627, p = 0.533$). The mean relative prey mass (RPM) for snakes that successfully consumed Sålí was almost one-third of its own mass ($31.5 \% \pm 2.0$). The smallest RPM value came from a prey item weighing only 7.2% of the mass of its predator, while the largest RPM value was found when a 90-g snake successfully ingested a Sålí fledgling that weighed 79.9% of its mass (71.9 g; Figure 4). In one exceptional case, a BTS consumed two Sålí fledglings in one meal (resulting RPM = 67.2%), whereas in all other cases only a single fledgling was consumed per meal.

2.5 Discussion

In this study, we documented that just under half of the radio-transmitted birds predated by snakes were not successfully ingested. This figure is likely an underestimate because some of the mortalities attributed to cats may have initially been unsuccessful snake ingestion attempts, as we found cats to be scavengers at our study site. Furthermore, we found that while the size of prey in our sample does not predict the likelihood of successful ingestion by snakes, the size of the predator is predictive of successful ingestion. Specifically, snakes that successfully ingested Sålí were significantly larger than snakes in the overall population that are attracted to endothermic prey. Finally, the smallest snakes that successfully ingested Sålí attained very high relative prey mass values for their species (up to nearly 80%), indicating they may be approaching their “breaking point” (the threshold size for successful ingestion; Arnold, 1982). Although individual animals are known to occasionally consume prey that tax their anatomical limit for

prey size, the frequency at which such events occur has remained an open question (Hertz et al., 1988; Jayne et al., 2022). Our results add to a growing body of evidence demonstrating that, in certain ecological contexts, snakes routinely attempt to consume prey items beyond the upper limit of their maximal gape (Robbins et al., 2019; Shine & Sun, 2003), with fatal effects on the prey and no documented impacts on the predator.

The relative prey mass figures we measured are the highest ever recorded for brown treesnakes (Chiszar, 1990; Rodda et al., 1999), and among the highest for any colubrid snake species (Glaudas et al., 2019). This is particularly remarkable because volant birds, such as Sāli, have relatively low body densities compared to mammalian or reptilian prey (Jayne et al., 2022). Although our methods did not allow us to directly sample snakes that were unsuccessful in ingesting birds, our results strongly indicate that intermediate-sized snakes, the most abundant size class on the landscape (Figure 3), are likely responsible for the bulk of the unsuccessful ingestion events we observed. This inference aligns with the observations of Shine and Sun (2003) that small *Gloydius shedaoensis* regularly fail to swallow excessively large prey due to gape limitation. Our results therefore support the prediction of Feder and Arnold (1982) that snakes would routinely attack large prey items even if they are ingested only occasionally, at least in instances where subduing the prey entails limited risk of injury and low energetic costs. However, the results contradict the prediction that predators behaving optimally would avoid attacking prey larger than their gape limit (Christensen, 1996), although the extent to which predators adopt optimal foraging strategies outside of their native ranges remains an open question.

BTS on Guam were previously thought to predate all life stages of smaller bird species, but only eggs and nestlings of larger species, because they would be incapable of swallowing larger prey (McElderry et al., 2021; Savidge, 1987). Wiles et al. (2003) found a negative relationship between body size and date of extirpation in forest birds on Guam, with smaller birds disappearing first, but no such relationship when the sample was extended to include birds from other habitats also affected by BTS, such as resident seabirds. It may be that behavioural adaptations among some of Guam's larger species (e.g., communal

roosting in *Corvus kubaryi*, Wiles 1998), rather than reduced snake predation on larger birds, drove the relationship between size and persistence in the forest bird sample. We did not detect any relationship between body size of Sāli fledglings and BTS ingestion success in our study. However, our sample was restricted to a single species with a relatively narrow body mass range (60 – 86 g). We might expect a negative relationship between size and probability of ingestion to emerge over a wider range of prey sizes. Moreover, it is probable that snakes will generally not try to feed on prey that vastly exceed their gape limit, even if such attempts are known to occur occasionally (e.g., Fritts, McCoid & Haddock, 1994; Natusch et al., 2021). For example, Shine and Sun (2003) found that small *Gloydus shedaensis* regularly made feeding strikes at decoys too large for them to conceivably ingest, but that an upper threshold for eliciting strikes did exist (i.e., small snakes did not strike at the largest decoys). Therefore although the largest prey species on Guam may have reduced risk of predation, the willingness of BTS to attack prey items too large for them to swallow may preclude a size refuge for most native bird species. One strategy for recovering avian populations on Guam has proposed focusing control efforts on the removal of the largest snakes on the landscape, in order to remove those individuals capable of consuming birds (e.g., Klug et al., 2021). However, our study demonstrates that snake management for bird restoration would need to account for fatal predation attempts by snakes too small to successfully ingest their prey. This is particularly important in light of the results of McElderry et al. (2022), which indicate that reintroduced native bird populations on Guam will have extremely low predation thresholds to allow population establishment.

Our results favour the suggestion that the benefit to predators of attempting to consume large prey items may outweigh the inherent risk of such behaviour if the potential energetic gain is substantial (Arnold, 1993; Natusch et al., 2021). Risk of asphyxiation may be considerable for snakes that attempt to consume oversized elongate (but not gape-limiting) prey, such as other snakes or amphisbaenians (e.g., Caramaschi and de Niemeier, 2012), which would cause unremitting pressure on the lung for the entire consumption attempt. Indeed, Collins and Rodda (1994) found that feeding BTS mice that were stitched together end-

to-end (weighing 52% of the snake's body mass) caused near-universal regurgitation and 2 fatal cases of asphyxiation in a sample of 12 snakes. However, despite documenting over 170 BTS ingestion attempts, with most of the successful attempts attaining high relative prey mass values ($> 30\%$), we did not encounter any BTS that died while attempting to ingest Sáli. Two BTS (one of which had consumed two Sáli fledglings) died while regurgitating their meals in captivity; however, the regurgitation may have been triggered by handling stress (Crum, 2012). It appears that predation attempts on gape-limiting prey, regardless of whether ingestion occurs, may pose a relatively low risk to snakes, assuming the prey can be safely incapacitated.

If the energetic gain from successful ingestion of large prey outweighs the cost of unsuccessful attempts, then conditions may favour attempts where failure is a possible outcome. Feder and Arnold (1982) estimated that the metabolic cost of predatory activity to Terrestrial Garter Snakes (*Thamnophis elegans*) was less than 1% of the energy assimilated from the prey. Cruz-Neto, Andrade & Abe (1999) tested the aerobic metabolism of juvenile South American Rattlesnakes (*Crotalus durissus*) ingesting prey ranging from 10-50% of their body mass, and found that the energy needed for prey ingestion represented only 0.02% of the energy content of the largest prey, and that aerobic metabolism during ingestion was relatively more efficient for larger prey than for smaller prey. Similarly, Canjani et al. (2002) found that the energy spent by *Boa constrictor* to constrict, inspect, and ingest prey ranging from 5 to 40% of their body mass ranged from 0.21 to 0.11% of the energy assimilated from the prey, respectively. The energetic costs of prey handling and ingestion for snakes appear to be trivial compared to the potential rewards, and consumption of larger prey may be more efficient than consumption of smaller prey. The most energetically costly aspect of feeding by snakes is the digestive process, which can involve major up-regulation of gut function, particularly for species that feed infrequently (Jackson & Perry, 2000; Secor, 2008). Although evidence in this regard is mixed, it has been hypothesized that the major energetic investment involved in digestion may be another incentive for snakes to maximize the size of their prey (Glaudas et al., 2019; Secor & Diamond, 1998; Shine & Sun, 2003).

Evolutionary theory predicts that a high rate of unsuccessful predation attempts should be expected if attempts are cheap and prey is valuable (Abrams, 1989). The work of others demonstrates that ingestion attempts for snakes are cheap and that large prey is valuable, while our results confirm that unsuccessful ingestion of birds may be more prevalent, and less risky, than previously recognized. Certain aspects of Guam's ecology, such as a substantial size gap between reptilian and most endothermic prey (Savidge, 1988), may promote ingestion attempts by snakes on oversized prey. However, the fact that this phenomenon was previously unrecognized despite several decades of intensive research on BTS, alongside comparable results from other systems where the predators and prey have coevolved (Robbins et al., 2019; Shine & Sun, 2003), indicated that high rates of unsuccessful ingestion by snakes can easily remain undetected without dedicated monitoring of prey species. Indeed, the large proportion of unsuccessful ingestion attempts we recorded would not have been captured by traditional techniques such as dissection of museum specimens or regurgitation by palpation, highlighting the utility of alternative methodologies in acquiring a more complete picture of the outcomes of predation attempts (Glaudas et al., 2017). Intensive monitoring of both predator and prey species is crucial to gain a deeper understanding of the complexities of predator-prey interactions. Additional research in other systems would help to uncover the full scale of unsuccessful ingestion by predators and its importance in shaping ecological dynamics.

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Data availability

Virginia Tech data and code for this study are available at <https://github.com/EBL-Marianas/Sliming>. United States Geological Survey data are available at <https://doi.org/10.5066/P14Q2JCZ> (Goetz & Nafus, 2024).

2.7 Figures



Figure 1: (A) Large Brown Treesnake (*Boiga irregularis*) in the process of ingesting a CHunge' (White Tern, *Gygis candida*); photo credit: Nathan Sablan, public domain); (B) slimed (unsuccessfully ingested) adult CHunge' found incidentally; (C) slimed fledgling Sâli (Micronesian Starling, *Aplonis opaca*) found during telemetry work; (D) slimed Sâli adult found incidentally.

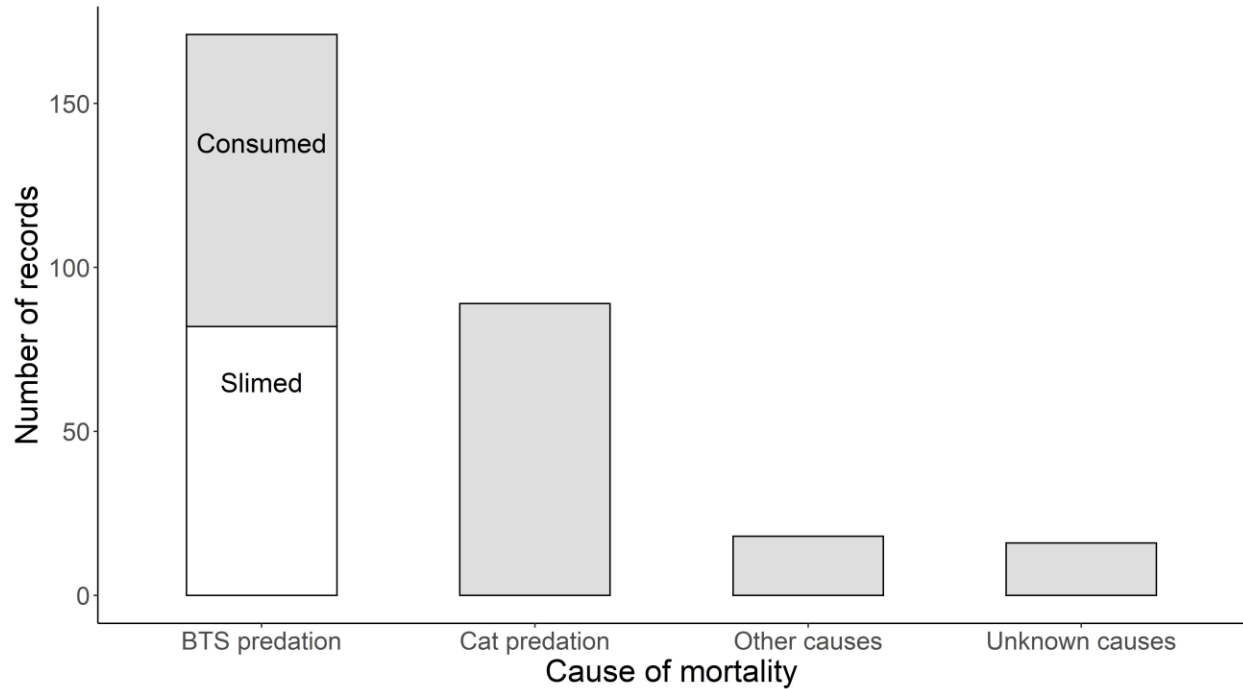


Figure 2: Records ($n = 294$ total) of Sâli (Micronesian Starling, *Aplonis opaca*) fledgling mortalities from Andersen Air Force Base, Guam, monitored via radio-telemetry between November 2019 and September 2022, by cause of mortality. BTS = Brown Treesnake (*Boiga irregularis*). Mortalities caused by unsuccessful ingestion by BTS (“slimed”, $n = 82$) are shaded white, all other categories are shaded grey. Mortalities identified as cat predation may represent direct kills or scavenging events. Other causes of mortality include starvation, exposure, road mortalities, and entanglement. The “unknown” category represents situations where it was not possible to determine the cause of mortality.

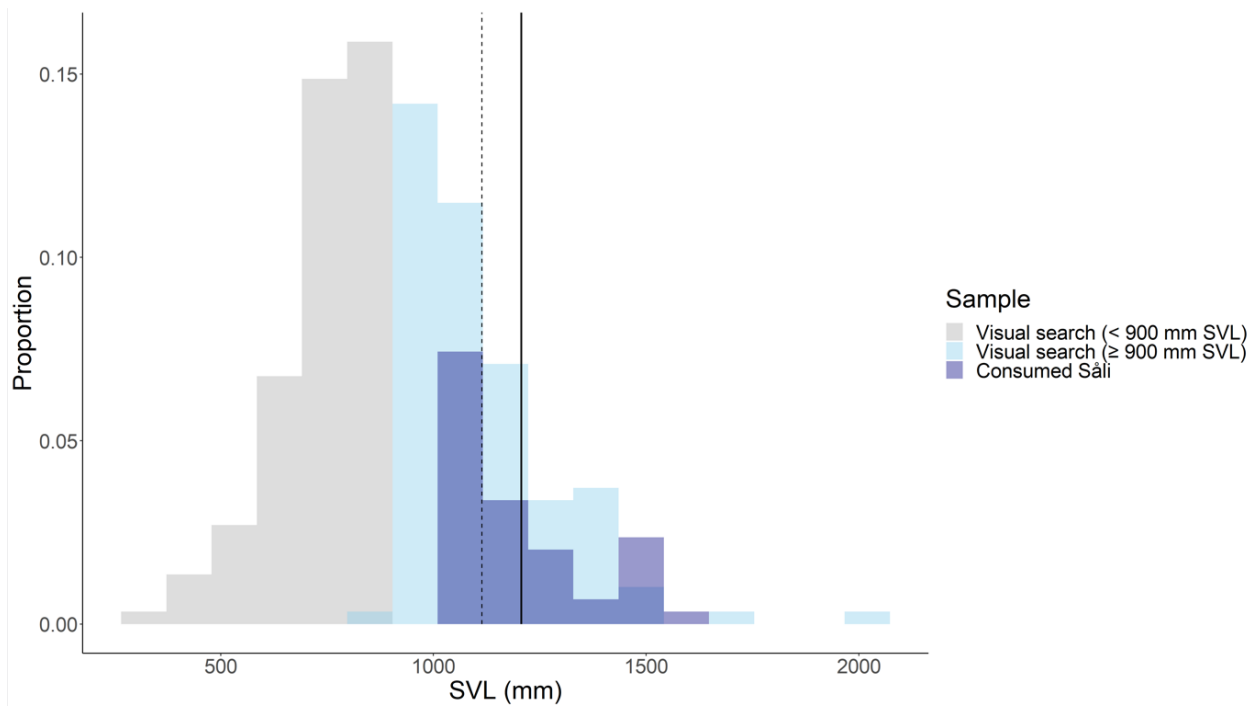


Figure 3: Histogram of snout-vent length (SVL, mm) of BTS (Brown Treesnake, *Boiga irregularis*) found during visual searches across the study site (grey, and light blue), and BTS that were captured after they successfully ingested Sâli (Micronesian Starling, *Aplonis opaca*) fledglings (dark blue). The dotted vertical black line represents the bootstrapped mean (1114 mm SVL; 95% confidence intervals: 1068 – 1165 mm); the bold vertical black line represents the mean SVL of the sample of BTS that successfully ingested Sâli (1206 mm). The threshold used to represent the minimum size of BTS attracted to endothermic prey was 900 mm SVL; BTS smaller than 900 mm SVL (grey bars) were excluded from the bootstrapping analysis. The y-axis indicates the proportion that each class represents relative to all sampled snakes.

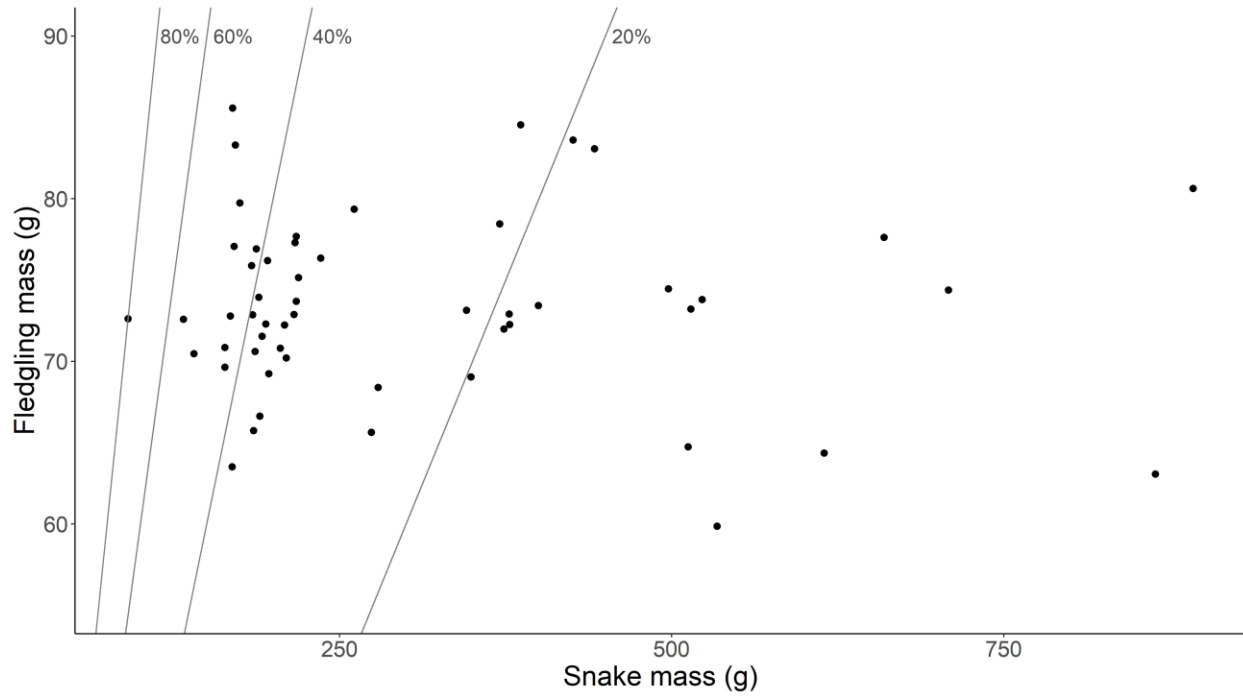


Figure 4: Scatterplot of BTS (Brown Treesnake, *Boiga irregularis*) mass (g) versus Sali (Micronesian Starling, *Aplonis opaca*) mass (g), whereby each point represents a relative prey mass (RPM = prey mass/predator mass) value for a BTS that successfully ingested a Sali fledgling. The grey lines represent the thresholds for RPM values of 20, 40, 60 and 80%, and points to the right of those lines have RPM values below those respective thresholds. A point with RPM of 0.67 (67%) was excluded from this graphic because the snake ingested two fledglings in a single meal.

CHAPTER 2:

Invasive snake drives trade-off in nest site selection for an island passerine

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Keywords: Clutch size; nest success; fecundity; fledgling survival; invasive species; life history; reproduction; trade-offs.

3.1 Abstract

For egg-laying animals (e.g. many reptiles, birds), the selection of an oviposition site has important fitness consequences. Parents need to balance risks to themselves, their eggs, and future offspring in their choice of a nest site. Invasive species present a novel threat to many native egg-laying species, and may change the optimal conditions for nest site locations. We monitored 70 Sáli (Micronesian Starling, *Aplonis opaca*) nest boxes on the tropical island of Guam, where invasive Brown Treesnakes (*Boiga irregularis*) have caused the extinction of most of the native avifauna. We collected data on the outcome of 821 nesting attempts and the survival of 461 fledglings between 2019 and 2022. Sáli nesting closer to the forest had more yearly nesting attempts than those farther from the forest. Conversely, we found that fledgling survival was higher the farther their natal nest box was from the forest. Clutch size, nestling condition (as measured by mass) and nest success did not vary with distance to forest. We suggest that a trade-off exists between a high energetic cost of long parental commutes to foraging areas at nest sites farther from the forest edge, leading to lower overall reproductive output per year, albeit with similar nestling condition and nest success, and a decreased risk of fledgling predation by Brown Treesnakes at those same sites, leading to higher fledgling survival. This relationship could inform the conservation management of this locally-endangered species, as well as other species with landscape-level variability in fecundity and risk of predation.

3.2 Introduction

Trade-offs have been central to the development of life-history theory (Williams 1966). Trade-offs occur when benefits at one life-history stage are linked with detrimental effects at another (Roff 2002). The cost of reproduction, which entails balancing potential fitness benefits with risks to survival and future reproduction, is the most prominent of all life-history trade-offs (Stearns 1989). Reproductive trade-offs are at the root of the astonishing variety of animal life-history strategies in terms of the frequency of reproduction and the number and size of offspring (Roff 2002). For egg-laying animals, such as insects, fish, reptiles and birds, the location and characteristics of the oviposition site can have important fitness consequences for parents and offspring (Refsnider and Janzen 2010). In freshwater turtles, for example, female turtles may prioritize their own survival over nest success when predation risk is high (Spencer 2002). Likewise in long-lived avian species, such as many tropical birds, adults are expected to prioritize their own survival over that of their offspring (Martin 1996, Ghalambor & Martin 2001).

Trade-offs may also exist between different early life-history stages, such that the factors promoting fecundity may therefore be different than those that promote offspring survival. For example, Flaspohler et al. (2001) found that ovenbirds (*Seiurus aurocapillus*) nesting near the forest edges had larger clutches but faced higher predation pressure than those in the forest interior. This may particularly be the case in altricial bird species, where fledglings continue to receive parental care for an extended period after leaving the nest. However, many avian studies equate nest success with the survival of eggs and hatchlings, while neglecting the effects of nest site selection on the highly vulnerable fledgling stage (Streby et al. 2014a). The fledgling stage is generally cryptic and technically challenging to study, likely contributing to its importance in nest-site selection having been largely overlooked (Streby et al. 2014a). In recent years, radio-telemetry studies have begun to reveal trade-offs in nest-site in certain bird species, where the factors that promote survival of eggs and hatchlings are opposed to those that promote fledgling survival (Streby & Andersen 2011, Streby et al. 2014b).

It is well-established that habitat quality can have important effects on avian productivity, and studies have shown that habitat can influence individual components of avian reproduction such as clutch size, nest success, and fledging survival (Armstrong & Ewen 2002, Armstrong et al. 2005, Hartmann et al. 2017). Habitat quality, for example, may be associated with differences in food availability, requiring individuals in lower quality habitat to travel longer distances for food. Stauss et al. (2005) found that Blue Tit (*Parus caeruleus*) pairs breeding in inferior habitat had double the foraging distances relative to pairs in superior habitat, resulting in smaller brood sizes. Seabirds nesting in dense colonies have substantially longer foraging distances than those in less dense colonies, with the latter scenario associated with lower energetic expenditure and relatively higher nesting success (Oppel et al. 2015). Nest site location is therefore tied to reproductive success by anchoring parents into a particular set of circumstances in which they need to gather resources to sustain themselves and their offspring throughout the full nesting and post-fledging period.

In many instances, the factors contributing to reproductive trade-offs appear to be caused or aggravated by anthropogenic habitat modification. Under specific circumstances, human modification of the landscape can alter avian habitat in such a way that their preferred habitat becomes an “ecological trap” where their fitness is reduced compared to other available habitat (Robertson & Hutto 2006, Suvorov & Svobodová 2012, Hale & Swearer 2016). For example, Great Tit (*Parus major*) nesting in forest patches damaged by invasive insects have equal clutch size but lower nest success and nestling condition than those in healthy forests (Krams et al. 2021). Moreover, it is suspected that many species have become relegated to suboptimal habitat when anthropogenic effects, such as the introduction of invasive predators, drive them from areas of more suitable habitat (Kerley et al. 2012). However, studies of avian reproduction that include data on fledgling survival remain relatively scarce, and particularly so in tropical, multi-brooded species (Streby et al. 2014a).

Here, we investigate the possibility of a trade-off between fecundity and fledgling survival in a locally-endangered tropical bird species, the Sāli (Micronesian Starling, *Aplonis opaca*). The island of Guam, in

the western tropical Pacific, has lost the majority of its native avifauna to the effects of an invasive predator, the Brown Treesnake (*Boiga irregularis*; hereafter BTS) (Savidge 1987). Only two breeding native forest bird species remain on the island, including the urban-tolerant Sâli (Wiles et al. 2003). Although they were historically widespread in forested habitats, Sâli on Guam currently nest and roost exclusively in developed areas (Jenkins 1983, Savidge et al. 2022). However, most of their foraging does not occur in urban areas due to a lack of feeding opportunities. Instead, they make directed foraging trips into surrounding forests during daylight hours when BTS are inactive (Pollock et al. 2020, Kastner et al. 2021). When Sâli are nesting, they commute repeatedly to the forest throughout the day to feed between incubation shifts or provisioning trips, with birds nesting farther from the forest making proportionally longer trips. The importance of different life history stages varies across bird species depending on factors such as their longevity (Sæther & Bakke 2000). In Sâli, adult survival appears to be high overall, while fledglings experience a very high mortality rate (74.4 %; Pollock et al. 2019, Nguyen et al. 2023). Therefore, current evidence suggests that survival at early life history stages may be particularly important for Sâli demography. Pollock et al. (2019) found that fledglings from nests closer to the forest were more likely to be predated by BTS, and that many Sâli fledglings are also predated by cats (*Felis catus*). Many Sâli nest in cavities in anthropogenic structures that are relatively inaccessible to potential nest predators, including an array of predator-proof nest boxes which we monitored at our study site (Savidge et al. 2022). The lack of nest predation allowed us to test the trade-off at early life history stages associated with foraging distance against survival at the fledgling stage.

We monitored Sâli nesting attempts and fledgling survival at their main breeding site in northern Guam and assessed how five components of reproductive fitness, namely (1) number of yearly nesting attempts, (2) clutch size, (3) nestling condition, (4) nest success, and (5) fledgling survival vary with the distance of nest sites to forest edge (“distance to forest”). In order to better understand the drivers of fledgling survival, we also investigated how mortalities due to the major predators of Sâli (BTS and cats) varied with distance to forest. We predict that pairs nesting farther from the forest edge will have lower

productivity (clutch size and number of yearly nesting attempts) due to their greater distance from foraging habitat. We also predict that the costs of longer foraging distances will be reflected in negative relationships between nestling condition and nest success and distance to forest. However, we expect higher fledgling survival at nest sites farther from forest due to lower predation risk at those sites; we predict a negative relationship between distance to forest and fledgling predation by BTS, but we do not anticipate *a priori* that fledgling predation by cats will be related to distance to forest.

3.3 Materials and methods

3.3.1 Study site and species

Our study took place on Guam (indigenous CHamoru name: Guåhan), the southernmost island in the Marianas archipelago and the largest in Micronesia. Guam experiences a tropical marine climate, with distinct dry (January–June) and wet (July–December) seasons. We investigated Sâli reproductive success on Andersen Air Force Base (AAFB), a military installation that covers approximately the upper third of the island’s northern plateau. AAFB is fringed by native limestone forest along its cliff lines, and is bordered by residential areas and mixed introduced forest to the south (Figure 1). Routine BTS control, primarily along the base perimeter, runways, and forest edges, has been ongoing on AAFB for several decades (Vice 2011). Additionally, targeted BTS control occurred in certain portions of the study site from October 2020 to July 2021 and April–November 2022, although it did not affect Sâli fledgling survival (see Chapter 3). The southeastern portion of the base, where the Sâli breeding area is concentrated, is intensively landscaped, and consists primarily of residential, commercial and administrative buildings surrounded by lawns dotted with isolated ornamental trees.

Sâli are medium-sized (~85g), omnivorous, cavity-nesting passerine birds in the starling family (Sturnidae). They are generally abundant throughout their range, which spans most island groups in Micronesia (Baker 1951). On Guam, however, they are locally endangered due to BTS predation, having

been reduced to an estimated low of 50–100 individuals in the early 1990s (Wiles et al. 1995). Our study site is located within their largest remnant population, which has recovered substantially and currently numbers approximately 1,500 individuals, (Pollock et al. 2022). While our study population breeds and roosts exclusively in urbanized areas, they forage widely in surrounding forests during daylight hours (Kastner et al. 2021). On Guam, Sāli breed year-round and mainly construct their nest sites in anthropogenic structures such as lamp posts, window shutters and nest boxes (Savidge et al. 2022). Nest boxes for Sāli, designed to be inaccessible to BTS and other potential predators, have been installed at the site since late 2015 (Savidge et al. 2022). Sāli pairs exhibit high nest fidelity, repeatedly nesting throughout the year in the same nest or in clusters of adjoining nests, which they vigorously defend from intruders (Suckow et al. 2022).

3.3.2 Nest and fledgling survival monitoring

We monitored Sāli nesting activity on AAFB between March 2019 and October 2022. Because nest type (e.g. natural cavity or nest box) and size are known to influence clutch size and possibly other measures of reproductive success (Stamp et al. 2002, Møller et al. 2017), we only monitored nest boxes for this study, which were identical in materials and dimensions, and designed to be predator-proof. There were 70 nest boxes at the site for the duration of this project, all constructed of PVC board and installed at 3 m in height on smooth concrete streetlamp poles isolated from any overhanging vegetation. The nest boxes ranged from 41 m to 942 m from the forest edge ($\mu = 342 \pm 234$ [standard deviation] meters) (Figure 1). We checked all nest boxes every 14 days to assess their activity status. The average incubation period for Sāli is 14.2 days (Savidge et al. 2022), therefore our nest check protocol allowed us to find the vast majority of nests during the incubation phase. We checked active nests (containing eggs or nestlings) twice per week to track development. Sāli generally lay eggs on consecutive days, and we considered the clutch size as the maximum number of eggs laid in a single bout of egg-laying (range 1–4 eggs, $\mu = 2.19 \pm 0.55$ [standard deviation]; Savidge et al. 2022). Occasionally, Sāli lay a new clutch on top of a previous

clutch of unhatched eggs, in which case we considered the clutch size as the number of newly laid eggs, not the total number of eggs in the box.

From December 2019 to October 2022, we banded all nestlings approximately two days prior to their expected fledge date (i.e. 22-23 days post-hatching) with a size 2 or 3 U. S. Geological Survey metal band and a unique combination of three Darvic color bands. At a majority of nests (72%), we also attached a radio-transmitter to one or more randomly-selected nestlings per brood using a modified leg-loop harness (Rappole & Tipton 1991). The transmitters we deployed (BD-2, Holohil Systems Ltd., Carp, Ontario, Canada; or PowerTag, Cellular Tracking Technologies [CTT], Rio Grande, New Jersey, USA) had a pulse rate of one pulse per three seconds, and expected battery lives of 175 days and 46 days, respectively. To avoid any negative impacts on fledgling mobility, we ensured that harnesses were properly fitted and that the combined mass of the bands, harness and transmitter corresponded to less than 4% of the nestling's body mass (Barron et al. 2010).

We began survival checks the day following transmitter attachment, and continued until transmitter failure or confirmed mortality of the fledgling. Fledglings were checked daily for the first 2 weeks after leaving the nest, 3 times per week for the following 2 weeks, and weekly thereafter. We used hand-tracking using radio-telemetry receivers (R1000, Communications Specialists, Orange, California, USA; or Locator, CTT, Rio Grande, New Jersey, USA) connected to 3- or 4-element Yagi antennas to obtain visual resights of fledglings, confirming their identity via their unique color-band combinations. In the case of fledgling mortality, we assigned the cause of death as (1) BTS, if the fledgling was located inside a snake, if it was found "slimed" (i.e. dead with its head and nape covered in a mucous coating; Kastner et al. 2024), or if its transmitter was found encased in BTS fecal material; (2) cat, if only feathers and/or feet were found remaining, generally accompanied by a broken transmitter harness; and (3) other, if the available evidence pointed to a different source of mortality (e.g. starvation, entanglement), or if insufficient evidence was available to conclusively assign a cause.

3.3.3 Statistical analyses

We conducted all analyses in program R (v4.2.2) implemented in R Studio (RStudio 2023.06.1; R Core Team 2022). We used packages *tidyverse* (Wickham et al. 2019), *plyr* (Wickham 2011) and *lubridate* (Grolemund & Wickham 2011) for data manipulation; *ggplot2* (Wickham 2016) for graphing; *glmmTMB* (Brooks et al. 2017), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), *emmeans* (Lenth 2023) and *performance* (Lüdtke et al. 2021) for fitting and testing mixed models; and *ggResidpanel* (Goode and Rey 2019) for assessing model fit. We simplified all models by removing non-significant interactions but retaining all main effects, applying Wald tests to assess significance (accepted at $\alpha = 0.05$). We conducted *post hoc* tests using pairwise comparisons with least-squared means. All summary statistics are presented as mean (μ) \pm standard deviation (SD) unless noted otherwise.

Following Suckow et al. (2022), we removed Sâli pairs exhibiting chronic nest failure (> 75% nesting attempts unsuccessful) from the dataset. Chronic nest failure would be likely to inflate their yearly number of nesting attempts, and potentially decrease clutch size due to repeated re-nesting (Farnsworth et al. 2001). Given the potential for variable environmental conditions to affect breeding effort across years and also within years, we also included sampling year (factor) and day of the year (numeric, ranging from 1 to 366) as fixed effects. Sampling year has four levels (2019, 2020, 2021, and 2022) in the models for nesting attempts per year and clutch size. Because we only began banding nestlings and radio-tracking fledglings in late 2019, we included 3 years of data (2020, 2021, and 2022) in the models for nestling mass, nest success and fledgling survival, removing the few data points from December 2019. To improve model fit, we centered and scaled the distance to forest covariate.

To assess whether the number of nesting attempts per year is related to the distance of a nest box or pair of boxes used by the same Sâli pair (hereafter referred to as “nest site”) to the forest edge, we constructed a generalized linear mixed model (GLMM) with a Poisson error structure using package *lme4*. We added nest site ID as random effect in the GLMM, to account for repeated measures from the same breeding pairs over time. We included an interaction between distance to forest and year (4 levels) in our initial model formulation.

We employed a similar approach to evaluate the relationship between clutch size and distance to forest. We constructed a GLMM with a zero-truncated Poisson error structure (clutch size cannot be zero) using package *glmmTMB*, with a three-way interaction between distance to forest, year (4 levels), and day of the year in the initial formulation, and nest site ID as a random effect.

The relationship of nestling mass to distance to forest, year and sampling date was assessed using a linear mixed model using package *lme4*, with nest site ID as a random effect, and a three-way interaction between distance to forest, year (3 levels) and day of the year in the initial model structure.

We tested the relationship between nest success and distance to forest by constructing a GLMM with a binomial error structure using package *glmmTMB*. Following Pollock et al. (2019), we defined a successful nest as one where at least one nestling attained fledging age. The response variable was the binomial outcome of the nest, with successful nests coded as (0) and failed nests as (1). We included a three-way interaction between distance to forest, year (3 levels) and day of the year in the initial formulation, and nest site ID was included as a random effect.

We analyzed the survival of fledglings at each nest site using a GLMM with a binomial error structure in package *glmmTMB*. The response variable for each individual represented a daily value for survival (0) or mortality (1). Additionally, we conducted two parallel analyses to assess the probability of BTS and cat predation of fledglings by coding BTS or cat predation as (1) and all other outcomes (including predation from the other predator or other sources) as (0). For each analysis, we included distance to forest, year, and day of the year as fixed effects, initially fit as a three-way interaction. Candidate random effects for these models were a unique animal ID, clutch ID and nest box ID, and all combinations of those factors. We chose clutch ID as it accounts for repeated sampling of the same individual, as well as sibling effects in instances where we tracked multiple fledglings per clutch.

3.4 Results

We monitored 821 Sáli nesting attempts from 57 nest sites. After filtering for nest sites where nesting pairs exhibited chronic nest failure, our dataset contained 699 nesting attempts from 49 sites. On average, there were 5.84 ± 1.41 yearly nesting attempts per site. Clutch size ranged from one to four eggs, and the mean clutch size was 2.09 ± 0.54 per attempt. 71.3% of nests were successful, in that they fledged at least one chick. We banded a total of 670 nestlings, who weighed 73.87 ± 5.81 g on average. We monitored 461 fledglings via radio-telemetry, of which 71 had an unknown fate, 126 survived until 22 days, and 264 died within 22 days (68% of known fate birds). Of the mortalities, 159 were attributed to BTS (60%), 82 to cats (31%), and 23 to other causes (9%).

The number of annual nesting attempts per site decreased with increasing distance to forest ($z = -3.03$, $p = 0.003$; Figure 2a). The relationship between the number of nesting attempts and distance to forest did not vary by year, and pairwise contrasts did not reveal any differences in the number of nesting attempts between sampling years (Table 1). Clutch size did not vary based on distance to forest ($p = 0.86$; Figure 2b), year and/or day of the year (Table 2). Nestling mass fluctuated significantly depending on the day of the year, and this relationship varied across years ($p < 0.0001$). However, there was no relationship between nestling mass and distance to forest (Figure 3; Table 3). Nest success did not vary based on nest site distance to forest ($p = 0.97$; Figure 2c), year, and/or day of the year (Table 4).

Fledgling survival, in contrast, was higher for individuals from nest sites farther from the forest ($z = -2.58$, $p = 0.01$; Figure 2d). Fledglings that left the nest earlier in the year also had consistently higher survival than those that fledged later in the year ($z = 2.40$, $p = 0.02$). Fledgling survival also differed between years, with lower fledgling survival overall in 2022 compared to 2020 (z ratio = -2.84 , $p = 0.01$) (Table 5). Likewise, fledglings from nest sites farther from the forest were less likely to be predated by BTS than those near the forest ($p = 0.0007$; Figure 4a), and BTS predation increased throughout the year ($z = 3.17$, $p = 0.002$). The overall rate of BTS predation was higher in 2022 than in 2020 (z ratio = -3.56 , $p = 0.001$) and in 2021 (z ratio = 2.90 , $p = 0.01$) (Table 6). Cat predation did not vary in relation to distance to forest (Figure 4b), year, and/or day of the year (Table 7).

3.5 Discussion

We have documented a trade-off in nest site selection for Sâli, whereby selection pressures are acting in opposite directions on different life stages of the species. As predicted, the number of yearly nesting attempts was highest at nest sites closer to the forest edge, while fledgling survival was lowest at those same sites. Contrary to our predictions, however, clutch size and nestling mass did not vary with the distance of nest sites to the forest. Likewise, nest success showed no relationship with distance to forest. Therefore, the principal trade-off in Sâli recruitment is between net fecundity and the probability of young surviving once they exit the nest. Comparable trade-offs across early life-history stages (e.g. between nest success and fledgling survival) have been demonstrated in other avian species (e.g. Shipley et al. 2013, Streby et al. 2014b), and Badyaev and Ghalambor (2001) suggest a broad trade-off between fecundity and juvenile survival for bird species across an elevational gradient. Streby et al. (2014a, b) predicted that trade-offs between fledgling survival and other avian early life history stages would be prove to be more widespread than currently recognized among birds, as researchers increasingly consider the contribution of fledgling survival to total fitness.

Our study is unique in documenting a driver of nesting frequency in a multi-brooded tropical bird species. Sâli pairs breeding closer to forest nested nearly continuously throughout the year, with approximately 1.6 times as many nesting attempts as those at the sites deepest in the urban interior. One factor driving to this trend may be the elevated predation rate experienced by fledglings at sites closer to the forest edge, which could elicit more frequent renesting attempts from those breeding pairs. Because Sâli continue to feed young for several weeks after they exit the nest, fledgling mortality, particularly early in the post-fledging period, would allow parents additional time to for repeated nesting attempts. However, another contributing factor is likely to be the elevated energetic demands of longer foraging trips for pairs nesting in the urban interior. Even marginal increases in parental provisioning effort have been shown to decrease

the number of breeding attempts by birds within the same or subsequent years (Martin 1987). At our study area, the breeding pairs at the most isolated nest sites have commuting distances up to 23 times longer than those closest to the forest edge, which is likely to put heavy demands on the interior-nesting birds' energy budgets. While their proximity to foraging areas might be expected to result in larger clutch sizes for pairs nesting closer to the forest, we did not find any difference in clutch size across nest sites. This finding suggests that rather than greater access to food being associated with larger clutch sizes as in temperate ecosystems (e.g. Högstedt 1980, Dhondt et al. 1992), it may instead allow birds to gain condition for repeated nesting attempts in tropical systems with a stable climate.

While Sâli pairs nesting farther from their foraging habitat produced fewer broods per year, their nestlings did not suffer in condition and their nest success was equivalent to those with shorter foraging commutes. Nestling mass fluctuated cyclically throughout our study period, likely in association with broad shifts in environmental conditions. We had anticipated that the increased energetic demands for Sâli breeding pairs living farther from the forest edge would come at a cost to nestling condition. Experiments involving brood enlargement indicate that increased parental investment in breeding can affect nestling quality (Nur 1984, Smith et al. 1989, Sousa & Marini 2013), and field studies have shown that nestlings at inferior quality nest sites can have lower mass than those in better habitat (Krams et al. 2021). As in our study, however, Stauss et al. (2005) found that nestlings in inferior habitat were in similar body condition as those in better habitat, even if the breeding adults had to fly double the foraging distances to provision them. The fact that all our nest sites consisted of predator-proof nest boxes, along with the even condition of the nestlings across the study site, likely contributed to the lack of variability in terms of nest success. If the nests were unprotected, it may be expected that vulnerable nests closer to the forest edge would experience higher mortality rates due to predation by BTS. Taken together, these results illustrate that despite the greater energetic demands on Sâli pairs breeding farther from the forest edge, they do not compromise on nestling quality.

Sāli fledgling survival was low overall in our study, and particularly so for fledglings whose nest sites were close to the forest edge. As is commonly the case in studies of post-fledging survival of altricial birds (Naef-Denzer & Gruebler 2016), the vast majority of fledgling mortality (91% in our study) was a result of predation. The most important cause of mortality to fledglings at our site was predation by BTS, a result which aligns with the earlier results of Pollock et al. (2019), who also found an increasing risk of BTS predation for fledglings closer to the forest edge. Although BTS are present across much of our study site, the areas of highest density appear to be towards the periphery of the site closer to the forest edges (see Chapter 3). Bait-take rates by BTS are also higher along forest edges, and negligible in the urban interior, suggesting encroachment into the site by forest-dwelling snakes (Siers et al. 2023). Elevated predation rates are frequently recorded within edge habitats (Andrén 1995), and indeed may be mediated by higher snake activity in systems where they are important predators (Carfagno et al. 2006). Contrastingly, the risk of cat predation, which accounted for nearly one third of fledgling deaths, appeared to be spread evenly across our study site and did not vary over time. Cat control is a global priority in the management of island biodiversity (Nogales et al. 2013), and would likely produce immediate dividends for fledgling survival at our site.

Beyond distance to forest, we found that fledgling survival rates varied both seasonally and between years. Again, this effect appears to be related to largely driven by BTS predation, with the highest levels generally occurring throughout Guam's rainy season (June–December). Although seasonality in BTS activity has not been well characterized, tangential evidence does suggest a relationship with rainfall. For example, the frequency of BTS sightings during visual surveys, snakebites, and power outages (regularly triggered by BTS) all appear tied to rainfall and generally increase in the latter half of the year (Rodda et al. 1999). While our finding that fledgling survival decreases throughout the year is not unique, most previous studies have taken place in temperate ecosystems where the nesting season is not continuous (Naef-Denzer et al. 2001). Gaining a better understanding of the phenology of BTS predation risk to birds will be helpful in planning the timing of predator control efforts.

Our results recall those of several other studies that have demonstrated trade-offs in avian nest-site selection related to their proximity to habitat edges (Flaspohler et al. 2001, Shipley et al. 2013, Streby et al. 2014b.). The situation in our case differs from previous studies, however, in that our study species has been almost entirely extirpated from its former range on Guam, and is persisting by roosting and nesting in a habitat separate from its foraging range (Pollock et al. 2022, Savidge et al. 2022). Breeding Sâli are therefore obliged to make regular commutes to their foraging grounds throughout the day between incubation shifts or feeding bouts, engendering a lifestyle more akin to a loosely colonial seabird than a typical forest passerine. However, many other taxa, avian or otherwise, have been pushed through climatic shifts or anthropogenic disturbance into a “refugee species” status (Kerley et al. 2012, Kuemmerle et al. 2012, Smith et al. 2024). A refugee species is defined as a species with a current realized niche that is restricted to suboptimal habitat, with optimal habitat only potentially accessible through conservation management (Kerley et al. 2012). For example, historic evidence indicates that 10 bird species in Australia have been extirpated from over 99% of their former range (Ward et al. 2022). It is probable that many such species, existing on the margins of their preferred habitat, are experiencing reproductive trade-offs similar to those of Sâli, where the areas of highest productivity coincide with an elevated mortality risk. Uncovering these trade-offs will inform conservation efforts by identifying management interventions that could improve reproductive outcomes, or desirable habitat features to seek at potential reintroduction sites where threats are managed.

Our findings highlight the importance of understanding threats across the life cycle of species of conservation concern. If we had monitored only Sâli nesting activity, we may have felt compelled to recommend that their nest boxes be placed as close as possible to the forest edge, in order to maximize the number of potential yearly breeding attempts. Importantly, however, we intend deepen our investigation by integrating our analysis across all early life stages of Sâli, in order to better understand the relationship between Sâli nest site selection and their fitness, and investigate whether an optimal zone exists in terms of the distance of nest sites to forest. Indeed, it is easy to come to misleading conclusions about species’

optimal habitat if their full reproductive cycle is not studied (Streby & Andersen 2011, Streby et al. 2014a.). At worse, this can lead to managing a species into an ecological trap, where they are drawn into areas that seem suitable at a superficial level but in fact contain unidentified threats (Shipley et al. 2013). It is therefore crucial to monitor the entire reproductive cycle of birds in order to fully understand how their recruitment varies on a landscape level, and how survival at different life history stages impacts population demography. Further research is particularly needed in tropical ecosystems, where the breeding ecology of many multi-brooded bird species remains largely unstudied.

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3.7 Figures

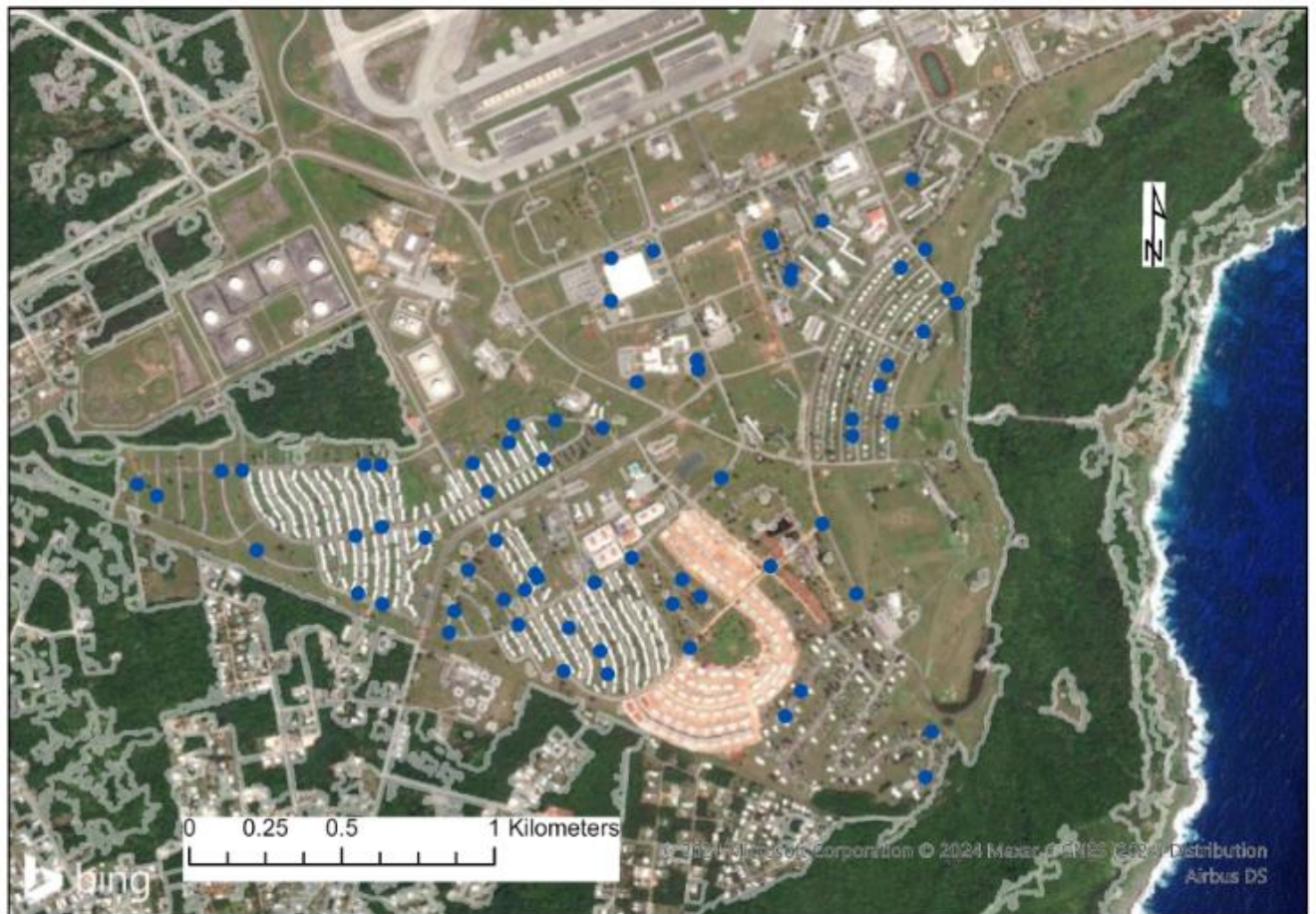


Figure 1: Map of the study area on Andersen Air Force Base, Guam, with Sáli (*Aplonis opaca*) nest boxes ($n = 70$) shown as blue dots. Forested areas are outlined in white.

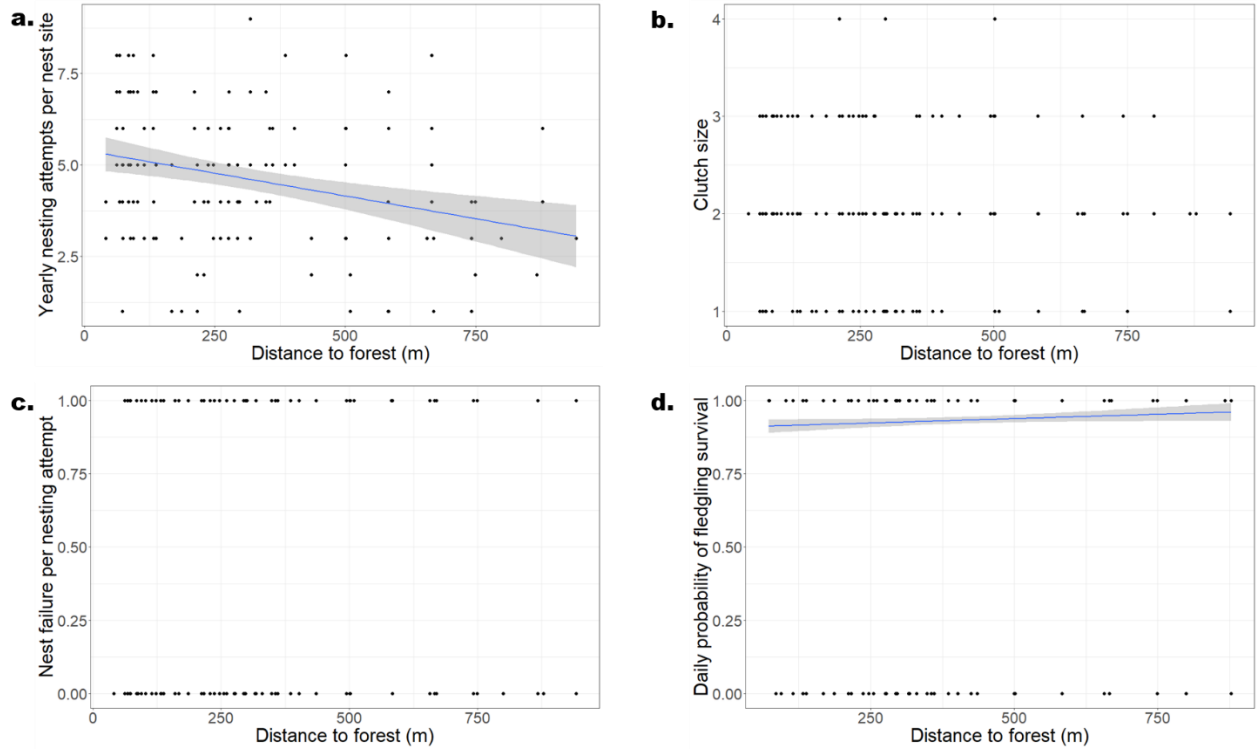


Figure 2: Relationships between (a) the number of yearly nestling attempts by Sâli (*Aplonis opaca*) breeding pairs, (b) mean clutch size, (c) nest failure per nesting attempt, and (d) daily probability of fledgling survival (mortality coded here as [0] and survival as [1], for illustrative purposes) and the distance of nest sites at our study site on Andersen Air Force Base, Guam, to the forest edge (in meters). The lines of best fit, calculated using linear models, are shown in blue with 95% confidence intervals shown in grey.

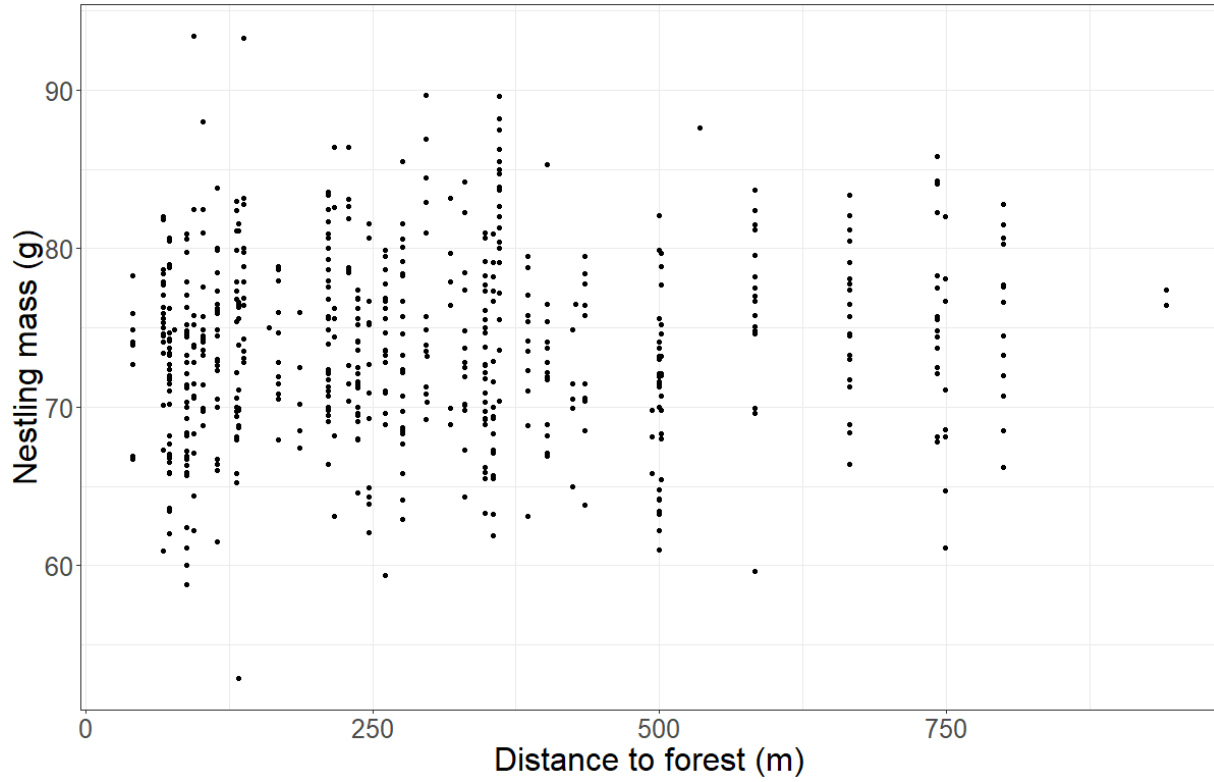


Figure 3: Relationship between Sâli (*Aplonis opaca*) nestling mass (in grams), sampled 2 days prior to their expected fledge date, and distance of their nest sites to the forest edge (in meters). Data were collected from nestlings in predator-proof nest boxes within the urbanized areas of Andersen Air Force Base, Guam.

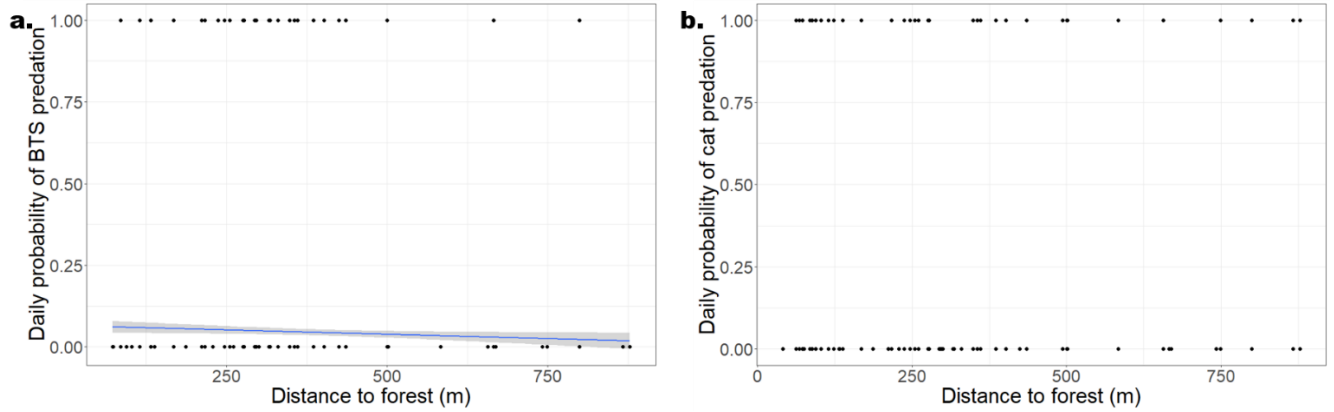


Figure 4: Relationships between (a) the daily probability of predation of Sali (*Aplonis opaca*) fledglings by Brown Treesnakes (*Boiga irregularis*), and (b) the daily probability of fledgling predation by cats (*Felis catus*), and the distance of nest sites at our study site on Andersen Air Force Base, Guam, to the forest edge (in meters). The lines of best fit, calculated using linear models, are shown in blue with 95% confidence intervals shown in grey.

3.8 Tables

Table 1: Fixed effects table for the generalized linear mixed model with Poisson error structure assessing the relationship between the number of yearly nesting attempts by Såli (*Aplonis opaca*), the distance of their nest sites to the forest (scaled), and sampling year, with nest site ID included as a random effect.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	1.35	0.10	13.32	<0.001
Scaled distance to forest	-0.12	0.04	-3.03	0.002
Year: 2020	0.26	0.12	2.17	0.03
Year: 2021	0.26	0.12	2.22	0.03
Year: 2022	0.11	0.12	0.92	0.36

Table 2: Fixed effects table for the generalized linear mixed models with zero-truncated Poisson error structure assessing the relationship between clutch size of Sâli (*Aplonis opaca*), the distance of their nest sites to the forest (scaled), sampling year, and day of the year, with nest site ID included as a random effect.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	0.82	0.009	9.19	<0.001
Scaled distance to forest	-0.004	0.03	-0.14	0.89
Year: 2020	-0.08	0.08	-1.02	0.31
Year: 2021	-0.08	0.08	-1.03	0.30
Year: 2022	-0.06	0.09	-0.75	0.43
Day in year	<-0.001	<0.001	-0.35	0.73

Table 3: Fixed effects table for the linear mixed model with Gaussian error structure assessing the relationship between nestling mass of S ali (*Aplonis opaca*), the distance of their nest sites to the forest (scaled), sampling year, and day of the year, with nest site ID included as a random effect.

	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	75.76	0.87	87.34	<0.001
Scaled distance to forest	0.29	0.42	0.69	0.49
Year: 2021	-4.45	1.10	-4.07	<0.001
Year: 2022	0.05	1.23	0.04	0.97
Day in year	-0.001	<0.001	-3.00	0.003
Year: 2021 * Day in year interaction	0.03	0.005	4.85	<0.001
Year: 2022 * Day in year interaction	<0.001	0.007	0.09	0.93

Table 4: Fixed effects table for the generalized linear mixed model with binomial error structure assessing the relationship between Sáli (*Aplonis opaca*) nest success, the distance of their nest sites to the forest (scaled), sampling year, and day of the year, with nest site ID included as a random effect.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	-1.17	0.30	-3.90	<0.001
Scaled distance to forest	-0.006	0.15	-0.04	0.97
Year: 2021	0.23	0.24	0.96	0.34
Year: 2022	0.33	0.26	1.24	0.21
Day in year	<-0.001	0.001	-0.64	0.52

Table 5: Fixed effects table of the generalized linear mixed model with binomial error structure assessing the relationship between daily Sâli (*Aplonis opaca*) fledgling survival, the distance of their nest sites to the forest (scaled), sampling year, and day of the year, with nest site ID included as a random effect.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	-3.49	0.31	-11.33	<0.001
Scaled distance to forest	-0.30	0.11	-2.58	0.01
Year: 2021	0.25	0.26	0.98	0.33
Year: 2022	0.85	0.30	2.84	0.004
Day in year	0.002	0.001	2.40	0.02

Table 6: Fixed effects table for the generalized linear mixed model with binomial error structure assessing the relationship between daily Sáli (*Aplonis opaca*) fledgling Brown Treesnake (*Boiga irregularis*) predation, the distance of their nest sites to the forest (scaled), sampling year, and day of the year, with nest site ID included as a random effect.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	-4.73	0.40	-11.87	<0.001
Scaled distance to forest	-0.49	0.14	-3.38	<0.001
Year: 2021	0.38	0.31	1.24	0.22
Year: 2022	1.27	0.36	3.56	<0.001
Day in year	0.004	0.001	3.17	0.002

Table 7: Fixed effects table for the generalized linear mixed model with binomial error structure assessing the relationship between daily Sâli (*Aplonis opaca*) fledgling cat (*Felis catus*) predation, the distance of their nest sites to the forest (scaled), sampling year, and day of the year, with nest site ID included as a random effect.

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	-8.91	1.22	-7.31	<0.001
Scaled distance to forest	0.02	0.40	0.04	0.97
Year: 2021	0.19	0.90	0.22	0.83
Year: 2022	0.52	1.05	0.50	0.62
Day in year	<-0.001	0.004	-0.24	0.81

CHAPTER 3:

Survival of avian prey following control of an invasive ectothermic predator

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Keywords: *Aplonis opaca*, *Boiga irregularis*, invasive species, fledgling survival, population regulation, predator control.

4.1 Abstract

Predator manipulation experiments are a crucial tool for determining whether predator populations have suppressive effects on the demography of prey. Invasive reptiles are known to have substantial negative impacts on native prey survival, but the effects of efforts to control their populations remain understudied. For example, no previous study has examined the survival response of avian prey to the suppression of a reptilian top predator. We used telemetry to monitor the survival of Sáli (Micronesian starling, *Aplonis opaca*) during their vulnerable post-fledging period (22 days) before and during targeted efforts to control their top predator, the invasive Brown Treesnake (*Boiga irregularis*). We monitored Sáli fledglings in areas receiving snake control as well as in untreated areas. Snakes were controlled within four plots in the Sáli breeding range using bait stations and traps deployed sequentially over the course of two years. Overall, 29% of fledglings were predated by snakes during the study. Fledgling survival was lowest in the first days after they exited the nest. Snake control was not associated with a change in fledgling survival rates from the pre-treatment baseline or in comparison to areas where snakes were not controlled. We did not detect a shift from snake predation of fledglings to other causes of mortality, and snakes remained the leading cause of fledgling mortality in both treated and untreated areas throughout the duration of the study. We hypothesize that the snake control measures we deployed were insufficient to increase fledgling survival or decrease the rate of snake-caused mortality. Our results suggest that some combination of improvements in tool attractiveness, deployment intensity or use of alternative tools will be needed to reduce predation pressure below the threshold required to improve avian survival.

4.2 Introduction

The relative importance of the various factors regulating animal populations has long been a hotly debated topic in ecology (Diamond 1975). Until the 1970s, intraspecific competition was believed to be the prevailing factor regulating population growth, but the importance of predation has been increasingly recognized in recent decades (Sih et al. 1985). This paradigm shift has been facilitated by the proliferation of *in situ* experimental manipulations, which involve monitoring the impact on prey populations of intentional alterations to the density of their predators (Krebs 1995). Such experiments offer a straightforward mechanistic approach for identifying the factors that influence population growth (Sih et al. 1985, Salo et al. 2010). Experimental manipulations have demonstrated that predators can have a considerable suppressive effect on prey populations (Sinclair & Krebs 2002, Salo et al. 2010). While this generalization applies to both native and introduced predators, the latter can have a particularly strong demographic influence on their prey (Salo et al. 2007, Salo et al. 2010).

Much of the evidence for the suppressive effects of introduced predators has accumulated from studies on islands. The magnitude of their impacts is clearly illustrated in the wave of extinctions that frequently follows the introduction of predators on islands (Steadman 2006). However, it has been proposed that once the most vulnerable species are “filtered” out by extinction, populations of the remaining native species on islands may be robust to the effects of introduced predators (Pimm et al. 1994, Balmford 1996, Blackburn et al. 2004). These suggestions are contested by evidence indicating that native island species respond more strongly to the control of introduced predators than do mainland populations to the suppression of their native predators (Salo et al. 2007). The complete removal of island invasives through eradication often allows the rapid recovery of native prey species (Jones et al. 2016), but when eradication is not logistically feasible, predator control can also be successful in enabling native species recovery (Moorhouse et al. 2003, Vanderwerf et al. 2023). However, predator management can also result in unintended consequences such as mesopredator release or other compensatory responses (Doherty & Ritchie

2017). Predator manipulation experiments allow the outcomes of such control efforts on prey species to be documented in a systematic and rigorous manner.

There has been a strong taxonomic bias towards mammalian predators in the focus of terrestrial manipulation experiments, whether on islands or in continental ecosystems. The most recent global meta-analysis included 116 studies, of which 69% manipulated mammalian predators, 21% focused on both mammalian and avian predators, 9% targeted avian predators and only 1% (a single experiment) studied reptilian predators (Salo et al. 2010). The lack of attention on reptilian predators is surprising, given the global importance of reptiles as predators (Vitt et al. 2003) and the increasing impact of snakes in particular as invasive predators (Savidge 1987, Dorcas et al. 2012, Piquet et al. 2021). The few studies on predatory snakes suggest they can have strong suppressive effects on populations of their mammalian or reptilian prey (Lindell & Forsman 1996, Calsbeek & Cox 2010, Campbell et al. 2012; see also Boback et al. 2022). However, there is a need for additional studies on predatory snakes in other systems, and investigations of their impacts on different classes of prey. For example, despite the importance of snakes as bird predators (Weatherhead & Blouin-Demers 2004), there have been no previous studies quantifying the impact of snake predation on avian recruitment.

The island of Guam, in the western Pacific Ocean, offers an ideal location for conducting an experimental manipulation testing the influence of snake predation on avian recruitment. Guam has no native snake species, but the invasive Brown Treesnake (BTS; *Boiga irregularis*) was accidentally introduced from Melanesia in the aftermath of World War II (Richmond et al. 2015). The subsequent spread of BTS led to the extirpation of the vast majority of Guam's avifauna (Savidge 1987), providing strong evidence that snake predators are capable of controlling populations of avian prey. Among the few extant native bird species, the Sâli (Micronesian Starling; *Aplonis opaca*) is greatly reduced in numbers and restricted to a small portion of its former range on the island. The Sâli's fledgling stage is particularly vulnerable to predation, with mortality rates exceeding 75%. BTS are responsible for the majority of predation events,

and feral or domestic cats are the other main predator of Sâli fledglings, accounting for around one third of deaths (Pollock et al. 2019).

Given strong conservation and biosecurity incentives, researchers have been actively developing a variety of methods for BTS control for several decades (Clark et al. 2018). The methods in most extensive use for operational control are trapping and the deployment of toxic bait. Many models of traps have been tested for BTS since the 1980s, and the current standard design is a modified minnow trap with live bait in a separate chamber (Rodda et al. 1999b, Vice et al. 2005). Toxic bait for BTS generally consists of a tablet of acetaminophen, which is lethal to snakes, delivered within a small piece of carrion and held within a short section of plastic tubing (referred to as a “bait tube”) designed to exclude non-target scavengers (Johnston et al. 2002, Lardner et al. 2013). Both trapping and baiting have demonstrated effectiveness at targeting BTS of the size classes likely to be predating avian prey in forested areas on Guam (Rodda et al. 2007, Lardner et al. 2013, Nafus et al. 2024). Most of the snakes poisoned or captured using bait tubes or traps, respectively, are medium-sized (e.g. 800–1100 mm snout-vent length [SVL]), while juvenile snakes are not impacted due to their preference for reptilian prey (Clark et al. 2018).

In this study, we used radio-telemetry to monitor the survival of Sâli fledglings before and during a period of active, spatially-targeted, BTS suppression. We attempted to reduce BTS density in four plots across the study area through the sequential deployment of toxic bait and live-capture traps, and monitored fledglings both inside and outside of areas experiencing predator control. We also conducted visual surveys of the BTS population in order to test whether the effect of control efforts depends on snake distribution and density at the site. We propose the following null hypotheses: (1) Sâli daily fledgling survival during BTS control will not differ from Sâli daily fledgling survival in treated areas prior to BTS control or in untreated areas (alternative hypothesis: Sâli daily fledgling survival during BTS control will differ from Sâli daily fledgling survival in treated areas prior to BTS control, or in untreated areas), (2) the rate of BTS-caused fledgling deaths in areas receiving BTS control will not differ from the rate of BTS-caused fledgling deaths in treated areas prior to BTS control, or in untreated areas (alternative

hypothesis: the rate of BTS-caused fledgling deaths in areas receiving BTS control will differ from the rate of BTS-caused fledgling deaths in treated areas prior to BTS control, or in untreated areas), and (3) the effect of snake control on fledgling daily survival and causes of mortality will be equivalent regardless of BTS density (alternative hypothesis: the effect of snake control on fledgling daily survival and causes of mortality will differ depending on BTS density). We predict that in all cases, the null hypotheses will be rejected and the corresponding alternative hypotheses will be accepted.

4.3 Materials and methods

4.3.1 Study site and species

4.3.1.1 Study site

We conducted our study between November 2019 and October 2022 on Andersen Air Force Base (AAFB), Guam (indigenous CHamoru name, Guåhan). Guam is the largest island in Micronesia, western Pacific, and the southernmost island in the Mariana archipelago. Guam experiences a tropical marine climate, with a dry season extending from January to June and a wet season from July to December. AAFB covers approximately 8,100 ha on Guam's northern tip. Our study took place within the roosting and breeding range of the largest remnant Sãli population on Guam, which is concentrated within the urbanized, southeastern portion of AAFB (Pollock et al. 2022). The landscape in this area is largely suburban, with detached homes and other buildings surrounded by expansive areas of lawn and isolated ornamental trees. There is a sharp boundary with primary limestone forest to the east, and mixed introduced forest interspersed with residential areas to the south (Figure 1). Predator-proof Sãli nest boxes have been installed on streetlamp posts throughout the study site since 2015 (Savidge et al. 2022). Routine BTS control has been ongoing on AAFB since the 1990s, primarily consisting of cage traps installed along the base perimeter fence, toxic bait along the forest edges and spot-lighting along fencelines (Vice 2011).

4.3.1.2 Prey species

Såli are a passerine species in the starling family (Sturnidae) endemic to Micronesia (Baker 1951). They are one of the most abundant bird species throughout most of their range, although the population on Guam is locally endangered due to predation by BTS, and is restricted to remnant populations in urbanized areas (Pollock et al. 2022). Their population on the island decreased to a low of 50–100 birds in the mid-1990s, but has since recovered to approximately 1,500 individuals, with over 90% of the population concentrated at our study site (Wiles et al. 1995, Pollock et al. 2022). On Guam, they breed throughout the year, and mainly use cavities within anthropogenic structures such telephone poles and window shutters for nesting (Savidge et al. 2022). Såli fledglings are relatively sedentary for the first three-to-four weeks after they leave the nest while they continue to receive post-fledging care from their parents, during which time they are extremely vulnerable to predation (Pollock et al. 2019).

4.3.1.3 Focal predator species

BTS are a nocturnal and mostly arboreal Colubrid native to northern Australasia, with a non-native range restricted to Guam and some of its offshore islands (Rodda et al. 1999a, Rodda & Savidge 2007, Barnhart et al. 2022). BTS are most abundant in forested areas, but they inhabit all terrestrial habitats on the island, including urbanized areas, where they attain relatively large sizes due to the availability of synanthropic prey like rats (*Rattus* spp.) and feral chicken (*Gallus gallus*) (Savidge 1991, Siers et al. 2017). Juvenile BTS principally feed on reptilian prey such as geckos and skinks, but they undergo an ontogenetic shift as they mature, switching to a diet principally comprised of birds, including Såli, and small mammals (Savidge 1988, Savidge et al. 2007). BTS on AAFB kill twice as many Såli as they successfully consume, indicating that relatively small snakes are routinely attempting predation of prey that is too large for them to swallow (Kastner et al. 2024).

4.3.2 Predator control

We conducted experimental BTS control within urbanized areas on AAFB using toxic bait delivered in bait tubes as well as live-capture traps. Bait tubes are plastic tubes designed to hold carrion bait for BTS and exclude the majority of non-target animals that might be attracted to the bait, such as crabs or monitor lizards (Mathies et al. 2011). The standard acetaminophen dose used in BTS baiting is an 80 mg tablet, which is lethal to nearly all individuals below 200 g of body mass (Siers et al. 2021). We provided two varieties of bait (18–30g mice and 25–35g chicken chicks) during this trial. While the most commonly used carrion in toxic baiting is small neonatal mice, we used bigger baits because it has been speculated that larger bait may be more suitable for BTS big enough to prey on Sâli (Siers et al. 2023). We offered avian bait because previous research indicates that BTS with a history of preying of birds tend to prefer bird-based baits over rodents (Nafus et al. 2021).

In the initial portion of the trapping phase of experiment, we used modified minnow traps with two inverted funnel-shaped entrances on either end of a cylindrical body constructed of metal mesh (Rodda et al. 1999b, Vice et al. 2005). This is the standard trap design used for capturing BTS, and is generally baited with a live mouse held in a separate chamber within the body of the trap, although alternative baits are sometimes used. Elevated traps were trialed during the latter portion of the trapping phase on the premise that traps placed in the canopy may be more effective at capturing BTS accustomed to arboreal foraging than traps placed at the standard operational height of ~1.5 m (S. Siers, USDA, personal communication).

The initial experimental design included four treatment plots, each approximately 9 ha in area, with two plots expected to harbor a high density of BTS and the other two predicted to have a low BTS density (Figure 1). One of the latter plots was removed from the study prior to the start of the live trapping phase because snake density was deemed too low in that plot to justify further effort. The remainder of the study area was considered untreated, and it included areas ranging from low to high densities of BTS.

Application of toxic bait in bait tubes began on 19 October 2020 and ended on 28 July 2021, with 50 bait tubes per plot installed on trees at least 20 m apart, and replaced twice per week. Two plots were baited

with mice and two with chicks for two weeks at a time, with the bait type changing every two weeks in a given plot. Live-trapping of BTS using standard live mouse lures began on 12 April 2022 and continued through the end of the study. Elevated mouse-baited traps were deployed from 21 July 2022 through the end of the study (Figure 2). The interruption in lethal control between the end of the baiting phase and the beginning of the trapping phase (Figure 2) was due to a pilot capture-mark-recapture trapping study conducted at the site from November 2021 to February 2022, and other logistical issues.

4.3.3 Fledgling survival monitoring

Såli fledgling survival was monitored continuously from 26 November 2019 to 30 September 2022. We therefore monitored fledgling survival for nearly 11 months before the beginning of the bait tube deployment, although we were unable to monitor the entirety of the trapping phase (Figure 2). The fledglings we monitored hatched in predator-proof nest boxes installed across our study site (Savidge et al. 2022, Kastner et al. 2024). We checked all nest boxes every 14 days to check for nesting activity, and visited active boxes (containing eggs or chicks) every 3-4 days to monitor development. We banded all nestlings approximately 2 days prior to their expected fledge date with a size 2 or 3 U.S. Geological Survey metal band and a unique combination of 3 Darvic color bands. We also attached radio-transmitters (BD-2, Holohil Systems Ltd.; or PowerTag, Cellular Tracking Technologies [CTT]) to one or more randomly-selected nestlings in the majority (72%) of clutches using a modified leg-loop harness (Rappole & Tipton 1991). We made sure that the total mass of the bands, transmitter and harness did not exceed 4% of the nestling's body mass in order to avoid any deleterious effects on their behavior (Barron et al. 2010).

Fledgling survival was checked daily for the first 15 days after they exit the nest, which is the period of highest mortality (Pollock et al. 2019), and three times per week thereafter. We only used survival check data for the first 22 days after a fledgling left its nest box, during which time they are largely sedentary and continue to be fed by their parents (Pollock et al. 2019). Because of their limited movement during that period, we equated fledgling daytime survival check locations with their expected roost location for

the following night. We used the Extract by Polygon tool in ArcGIS Pro to determine whether daily survival check locations were inside or outside treated areas because fledglings from a nest site inside a treated area sometimes crossed into untreated areas and vice versa.

We conducted hand-tracking using telemetry receivers (R1000, Communications Specialists; or Locator, CTT) and confirmed fledgling identity using their unique color band combinations. If the fledgling was found dead, we assessed the available evidence and assigned the cause of mortality as follows: (1) BTS predation if the fledgling was tracked inside a BTS, found killed but not ingested by a BTS (Kastner et al. 2024) or was gut-passed by a BTS; (2) cat predation, if we found the transmitter amongst scattered flight feathers, feet and bands; and (3) other, if a definitive cause of mortality could not be diagnosed, or if the available evidence pointed to a different cause (e.g. entanglement, starvation).

4.3.4 Brown treesnake visual searches

We included a measure of BTS density as a covariate in our fledgling survival analysis to test whether the effectiveness of predator control varies with the starting abundance of snakes. However, BTS density is notoriously challenging to accurately assess, because of the species' cryptic nature and variable detectability (Boback et al. 2020). Catch-per-unit-effort (CPUE), while not a measure of true density, can be used to generate a proxy measure for BTS density across the landscape (Boback et al. 2020). We therefore used visual surveys conducted across the study site to create a heat map of BTS CPUE. Between December 2019 and November 2022, trained observers searched trees within the experimental area using high powered headlamps (3200 lumen Wilma headlamp, Lupine Lighting Systems). We examined individual trees for a predetermined amount of time that varied depending on the structural complexity of the tree species (range: 0:15 and 3:00 mins). We also counted all snakes found incidentally on the ground between targeted searches of trees.

To avoid artificially inflating CPUE values, we only used data from trees that were surveyed for more than 10 minutes. In ArcGIS Pro, we use the kernel density estimator weighted by BTS sightings-per-unit-

effort for individual trees to create a heatmap, which autogenerated scales ranging from 0 to 17,956,364.

We then used the raster calculator function to rescale the layers to CPUE values between 0 and 1.

Because of the amount of survey effort it took to accrue sufficient resolution on CPUE data across the full study area, we were only able to generate a static measure of CPUE across the landscape and cannot accurately assess the impact of the predator control measures on CPUE.

We used the Extract Values to Points tool in ArcGIS Pro to associate a CPUE value to each individual Sáli survival check or mortality location. We only included sampling events with an associated CPUE value in our final dataset, thus survival checks for birds that ranged outside the core experimental area were excluded (33% of records).

4.3.5 Statistical analyses

All analyses and graphing were performed using R Statistical Software (v4.2.2; R Core Team, 2022). We used packages *dplyr* (Wickham et al. 2023) and *lubridate* (Gromelund & Wickham 2011) for data manipulation and package *ggplot2* (Wickham 2016) for graphing.

4.3.5.1 Fledgling survival

We compared fledgling survival rates between the treated and untreated areas during the pre- and post-treatment periods using a binomial mixed effects model run using package *glmmTMB* (Brooks et al. 2017). The nightly binomial response for each individual was survival (0/1). The fixed effects included in the model were a treatment/period factor with four levels (treated-pre, treated-post, untreated-pre and untreated-post), scaled BTS catch per unit effort (CPUE) value, and fledgling age ranging from zero (fledge date) to a maximum of 22 days. The age covariate was included because fledgling survival rates often change substantially over the first few days after a fledgling exits the nest (e.g. Yackel Adams et al. 2006, Pollock et al. 2019).

We hypothesized that the largest effect of predator control would be seen in areas with the highest BTS CPUE, because we anticipated that the relative decrease in BTS density from control efforts would be greatest in those areas. If that were the case, we would see a significant interaction between the variables for treatment/period and BTS CPUE. If BTS control is equally effective at all BTS CPUE levels, then we predict a significant effect of the treatment/period factor. Our initial model therefore contained an interaction term between the treatment/period factor and BTS CPUE.

We performed likelihood ratio tests using the drop1 function to determine the optimal random structure for the model. Potential random effects considered for the model included the nested categories of individual animal identity (AID; accounting for repeated measures of the same individual), clutch ID (to account for sibling pair groups), and nest box ID (to account for environmental effects of nest box locations, and genetic effects from the resident breeding pair). We tested all combinations of random effects, and found that clutch ID explained the greatest proportion of variance in the models. Clutch ID has the potential to account for repeated sampling of individual birds as well as sibling effects when multiple individuals from the same nest box were tagged.

We dropped non-significant interaction terms, and retained all fixed effects in the final model. We assessed differences of interest between factor levels of our categorical covariate (treatment type/period) with pairwise comparisons in package emmeans (Lenth 2023). To validate the model, we visually assessed for heterogeneity by plotting the Pearson residuals against the models' fitted values, and against the continuous explanatory variables (CPUE and Age). We used Wald Chi-Squared tests with $\alpha = 0.05$ to assess significance.

We first conducted the analysis on the full dataset containing the pre-treatment and both control (baiting and trapping) periods (Figure 2). We also repeated the analysis on truncated datasets that only included the pre-treatment and baiting periods, and the pre-treatment and trapping periods. Our reasoning for conducting both the full and the truncated analyses was to investigate the possibility of stronger responses to the baiting or trapping phases alone, since there was a hiatus between baiting and trapping that might

complicate the response when comparing the pre-treatment period to the entire period after control began. However, it is possible that the effect of the baiting phase would carry over through the hiatus and be compounded by the trapping phase.

4.3.5.2 Cause of mortality

We predicted that BTS control would lead to a decrease in BTS-caused mortality, even if an increase in compensatory causes of mortality resulted in the overall mortality rate to stay the same. Alternatively, BTS-caused mortality could remain constant if the snake control measures were not sufficient to elicit a response. We therefore analyzed changes in cause of mortality in the treated and untreated areas during the pre- and post-treatment periods using a separate binomial mixed effects model, again using package `glmmTMB` (Brooks et al. 2017). The nightly binomial response for each individual was mortality due to BTS or any other outcome (survival or mortality due to other causes). We hypothesized that the largest change in cause of mortality would be seen in areas with the highest BTS CPUE, because we anticipated that the relative decrease in BTS mortality due to control efforts would be largest in those areas. The fixed effects included in the model were, as with the survival analysis, a combined treatment/period factor, scaled CPUE, an interaction term between the treatment/period factor and CPUE, and fledgling age. Our processes for selecting the random component, validating and interpreting the model were the same as described for the survival analysis above.

4.4 Results

We attached transmitters to 345 Sâli fledglings within the study site between December 2019 and September 2022 (treated areas: 39 pre-treatment, 104 post-treatment; untreated areas: 41 pre-treatment,

161 post-treatment). Our final dataset included 2,700 fledgling nights, with 1,203 in treated areas and 1,497 in untreated areas. Fledglings were tracked between 0 days (mortality on same day as fledge date) and 22 days (threshold for dispersal date). Overall, 160 mortalities were confirmed, with 100 caused by BTS (63% of total mortalities), 47 caused by cats (29%), and 13 due to other causes (8%). BTS were the leading cause of mortality throughout the study site, both pre- and post-treatment (Figure 3).

4.4.1 Predator control

Overall, 16,400 toxic bait items were deployed throughout the baiting phase, consisting of 8,200 mice and 8,200 chicken chicks. Of these, 186 mice and 116 chicks were taken, for a total of 302 bait takes (1.89%). Bait take was higher in plots with a higher initial expected density of BTS (232 baits taken) than in plots with low expected BTS density (70 baits taken). Applying a 10.8% non-target take rate based on the results of a pilot study (Siers et al. 2023), this results in an estimate of 269 baits taken by snakes.

Ninety-nine traps (standard mouse-baited and elevated mouse-baited) were deployed in the three treatment plots during the trapping phase, for a total of approximately 19,305 trap nights. In total, 20 BTS were captured and removed from the treatment areas with these traps.

4.4.2 Fledgling survival

For the full dataset, our final model contained all of the initial fixed effects (treatment /period, CPUE and fledgling age), but with no interaction between treatment/phase and CPUE (Table 1). Thus, our prediction that BTS control in areas with high BTS CPUE would be more effective in reducing the probability of Sâli fledgling mortality was not upheld. In addition, pairwise comparisons did not reveal any differences in survival probability between treatment types or periods of interest (Figure 4). Most notably, survival in the treated areas in the pre-treatment phase did not differ from survival in the same areas during the

control phase ($p = 0.83$), survival in the untreated areas in the pre-treatment phase did not differ from survival in the same areas during the control phase ($p = 0.95$), and survival in the treated areas did not differ from survival in the untreated areas during the control phase ($p = 0.16$). Fledgling deaths were higher in areas with greater BTS CPUE, although the relationship was only marginally significant ($p = 0.06$). The probability of mortality decreased as fledglings increase in age ($p < 0.0001$; Figure 4), as expected from previous studies.

The results were qualitatively similar for the truncated datasets comparing the pre-treatment period to just the baiting or trapping phases. In all cases, survival was lowest in first days a fledgling exited the nest box. Survival did not vary across any treatment types or periods of interest when comparing the baiting or trapping phases to the pre-treatment baseline.

4.4.3 Cause of death

We found an interaction between treatment/period and BTS CPUE ($p = 0.005$). Our hypothesis that a greater change in BTS-caused mortality would occur in areas with higher BTS density was therefore upheld, although it was not in the direction predicted. Surprisingly, we found an increase rather than a decrease in BTS-caused mortalities in areas with higher BTS CPUE. We did not record a shift from BTS predation towards other causes of mortality. Overall, BTS-caused mortality was more prevalent at younger fledgling ages ($p = 0.003$).

4.5 Discussion

Contrary to our prediction, Sáli fledgling survival did not increase in response to control efforts targeted at their main predator, the Brown Treesnake. Moreover, we did not document a decrease in deaths caused by snakes relative to other causes of death as a result of BTS control, indicating that the lack of a response

in fledgling survival to BTS control was not the result in a compensatory shift from BTS predation to other causes of mortality such as feral cats. BTS remained the leading cause of mortality for Sâli fledglings in both treated and untreated areas throughout the duration of the study, with 20-40% of transmitterd fledglings predated by BTS in each phase of the experiment, a rate on par with previous studies of fledgling survival in this species (Pollock et al. 2019). Although a lack of a response in fledgling survival to BTS control measures would also be expected if BTS did not affect Sâli fledgling survival, that possibility can be rejected because of the continuing high rate of BTS-caused fledgling mortality. It thus appears that the control methods deployed were insufficient to reduce BTS density to a level that would allow an increase in fledgling survival.

While our predator manipulation experiment focused on BTS, the primary predator of Sâli, we highlight the importance of cat predation as a persistent threat to Sâli survival. Cats have consistently ranked as the second-most important predator for fledgling Sâli, being responsible for approximately 20 to 30% of predation events in this and previous studies (Pollock et al. 2019). Feral and domestic cats are a major threat to birds globally, and particularly so to island-endemic species (Medina et al. 2011, Loss and Marra 2017). In many systems, predation by mesopredators such as cats increases in a compensatory fashion when other predator species are controlled (Ellis-Felege et al. 2012). While we did not observe such an effect in our study, it is conceivable that cat predation could increase in importance if BTS densities were reduced further. Managers may consider multipredator control when undertaking future avian conservation or restoration projects on Guam. Removing multiple predators is a common goal of invasive species management, in order to avoid potential unintended ecological consequences from removing a single predator species in a multipredator system (Baker et al. 2020, Walsh et al. 2012).

Predator manipulation experiments regularly lead to positive demographic impacts for prey populations (Sih et al. 1985, Salo et al. 2010). Indeed, this has been the case in several previous experiments that manipulated predatory snakes with rodent and lizard prey (Lindell & Forsman 1996, Calsbeek & Cox 2010, Campbell et al. 2012). Nevertheless, a response from prey species is by no means a certainty, and

roughly a quarter of studies reviewed in a meta-analysis on the impacts on predator manipulation experiments reported no impact of predator control on prey populations (Salo et al. 2010). Broadly, high efficiency manipulations (those that had a clear effect on predator densities) produced a significantly greater effect on prey populations than those deemed as low efficiency, whose effect size did not differ from zero (Salo et al. 2010). In our study, bait take rates were substantial in treatment areas (estimated 269 snakes removed), and particularly in plots with higher estimated BTS density. Trapping yields were much lower (20 snakes removed), although it is unknown if the low capture rate is due to population suppression from the baiting phase or other factors. However, the extent to which BTS density was reduced in treatment plots is unknown because of the challenges associated with estimating total abundance of BTS (Rodda et al. 2007). It is often the case that predator densities need to be lowered to beyond a certain threshold before effects on prey populations are detectable (Choquenot & Parkes 2001). Indeed, McElderry et al. (2022) estimated that BTS contact rates would need to be exceedingly low (e.g. 0.0002 to 0.0006 nightly contacts) to allow population growth of native bird species on Guam. It thus appears probable that the control measures we deployed did not reduce the BTS population at our site beyond the threshold necessary for a detectable prey response.

There are other aspects of the experimental design that may have dampened the impact of our predator control efforts. For example, the treatment plots were relatively small, entailing a high edge to interior ratio. Although the extensive network of roads, open pavement and lawn at our study site likely act as barriers to BTS movement (Siers et al. 2014), it is probable that all treated areas in our study experienced some reinvasion pressure throughout the duration of the experiment. Bait takes were consistently highest along plot edges and particularly those that abutted forested areas, both during pilot work (Siers et al. 2023) and the toxic baiting phases. This suggests persistent encroachment into the urban area by forest-dwelling BTS, and potentially movement into treated areas from snakes outside the plots. An extended temporal gap between the bait tube and the trapping phases of our study likely increased the probability of reinvasion of the treated areas, and recruitment within the surviving resident BTS population.

Bait tubes and traps are mainstays of the BTS control toolkit, and they have important advantages and limitations that are pertinent to our study. Traps have been used extensively for several decades, while bait tubes have been incorporated into the operational control network more recently (Clark et al. 2018). Both tools offer the advantage of acting as relatively passive means of control, with maintenance only required every few days, and bait tubes have been found to be particularly cost effective (Clark et al. 2012). While neither tool targets juvenile snakes (Lardner et al. 2009), both tools are useful in targeting medium-sized BTS attracted to endothermic prey, the size class most likely to predate fledgling Sâli. Approximately half of BTS-caused Sâli fledgling mortalities are from snakes too small to swallow the fledglings (Kastner et al. 2024). While the exact size of the BTS responsible for such cases is unknown, it is probable that most would be within the size range susceptible to bait tubes and traps. The lethality of the standard toxicant used in bait tubes, an 80 mg acetaminophen tablet, diminishes for BTS with a body mass over 200 g (Siers et al. 2021). However, the large majority (~80%) of snakes that successfully consume fledglings (~52% of predation events) weigh more than 200 g (Wagner et al. 2018, Kastner et al. 2024). Therefore, most snakes that can successfully swallow Sâli at our study site would need to consume multiple doses of toxic bait to succumb to its effects (Siers et al. 2021). Moreover, carrion baits have also been shown to be less attractive to snakes in good body condition (Nafus et al. 2024), yet BTS that consume Sâli generally have excellent body condition (Wagner et al. 2018). Bait tubes and traps have also been shown to be less effective in areas with greater prey availability (Gragg et al. 2007, Siers et al. 2024). The particulars of the relationships between BTS control tool effectiveness, prey availability, and other site-specific factors remain to be uncovered, but it is possible that the relative abundance of prey at our site limited the impact of our intervention.

There are a number of potential improvements to our methodology that could be tested in future BTS control trials under similar conditions. These may include using control tools in concert rather than sequentially, increasing their density, using alternative tools (e.g. live-bird-baited cage traps, self-resetting kill traps, detector dogs), and integrating visual survey-based removals into the control toolkit (Nafus et

al. 2024). A major limitation of our study was that we did not have a direct measure of predator density against which to assess the impacts of control efforts, which is considered an essential precondition of successful manipulation experiments (Choquenot & Parkes 2001, Salo et al., 2010). Integrating visual surveys into the control program would address that issue, because they could be used to remove BTS and simultaneously survey the population (Siers et al. 2024). Alternative methods, including take rates from bait tubes, can be used as indices BTS density (e.g. Siers et al. 2020), but they are at risk of bias because of issues such as size- and population-dependent prey preferences. Visual surveys are also prone to some level of bias in terms of size-class-specific detectability, but they offer the best available tool for detecting, and removing, BTS of all size classes (Rodda et al. 2007, Christy et al. 2010).

Our study represents a step forward in managing BTS for avian conservation on Guam, and a first attempt at understanding how the control of reptilian top predators affects avian recruitment. While we did not find a response in Sâli fledgling survival to BTS control, our research offers clear management lessons. Bait tubes and traps, at the density deployed, are not sufficient to reduce BTS predation pressure below the threshold needed to produce a response in Sâli recruitment. Therefore, these tools will need to be used in a different configuration, at higher densities, or alongside alternative tools to produce a sufficient effect. Moreover, it is important to monitor not only the survival of the prey population, but also the impact of the management intervention on the predator population in order to confidently ascribe a mechanistic link between predator control and the prey response. Finally, managers may consider implementing multi-predator control in order to avoid compensatory increases in predation from sources beyond the main target predator.

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4.7 Figures

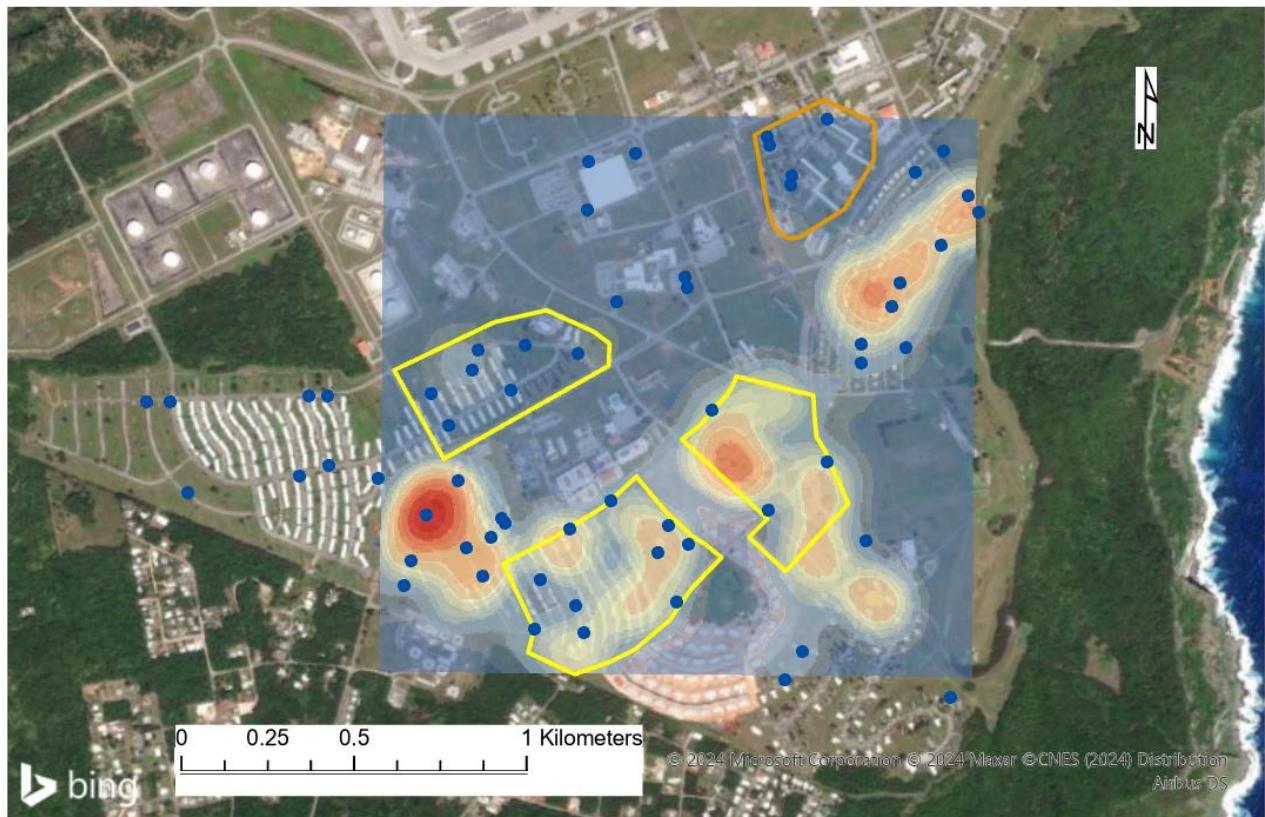


Figure 1: Experimental plots used in the bait tube deployment phases of the Brown Treesnake (*Boiga irregularis*) control experiment within housing and other developed areas on Andersen Air Force Base, Guam. Blue dots indicate Sali (*Aplonis opaca*) nest boxes at which fledglings were tagged for this study. The plots outlined in yellow were treated in both the bait tube and trapping phases of the experiment, whereas the plot outlined in orange was only treated during the bait tube phase of the experiment, then dropped because BTS CPUE was deemed too low to justify further effort. The heatmap spans areas where Brown Treesnake visual surveys were conducted and catch-per-unit-effort values computed, with warmer tones indicating higher CPUE. Sali fledglings in the yellow plots were considered to be in treated areas, and fledglings within the white box but outside the yellow plots were considered to be in untreated areas.

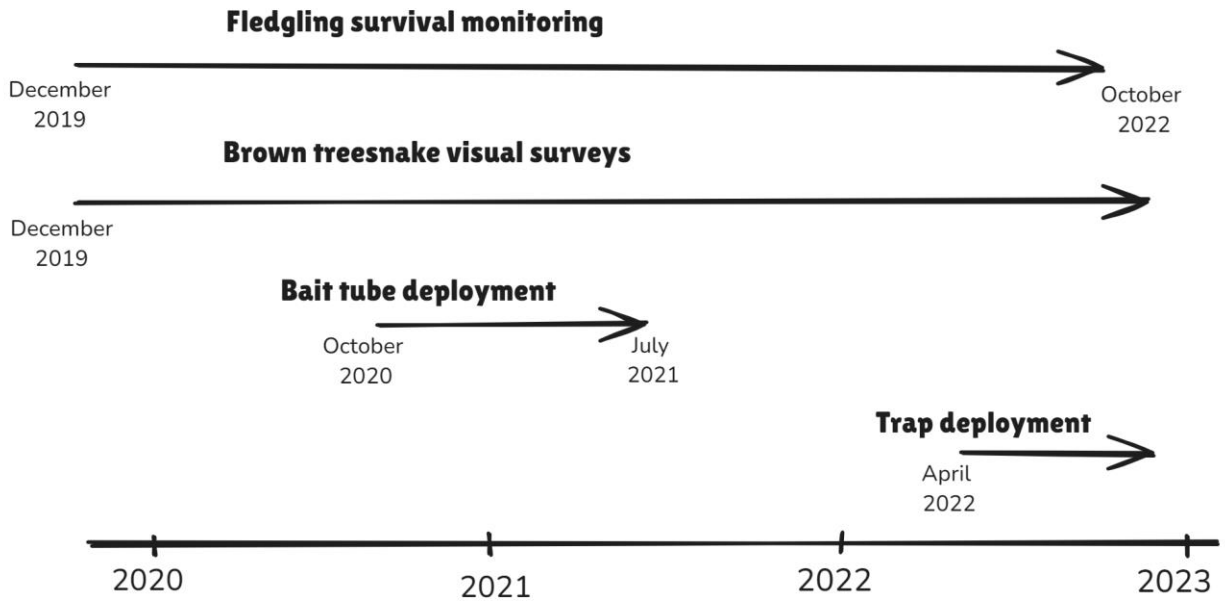


Figure 2: Timeline of data collection for the various phases of the predator manipulation experiment. Fledgling survival monitoring occurred from 26 November 2019 to 30 September 2022; Brown Treesnake surveys from December 2019 to November 2022; bait tube deployment using toxic bait from 19 October 2020 to 28 July 2021; and trapping using live mouse-baited traps from 12 April 2022 through the end of fledgling survival monitoring, and elevated mouse-baited traps from 21 July 2022 through the end of fledgling survival monitoring.

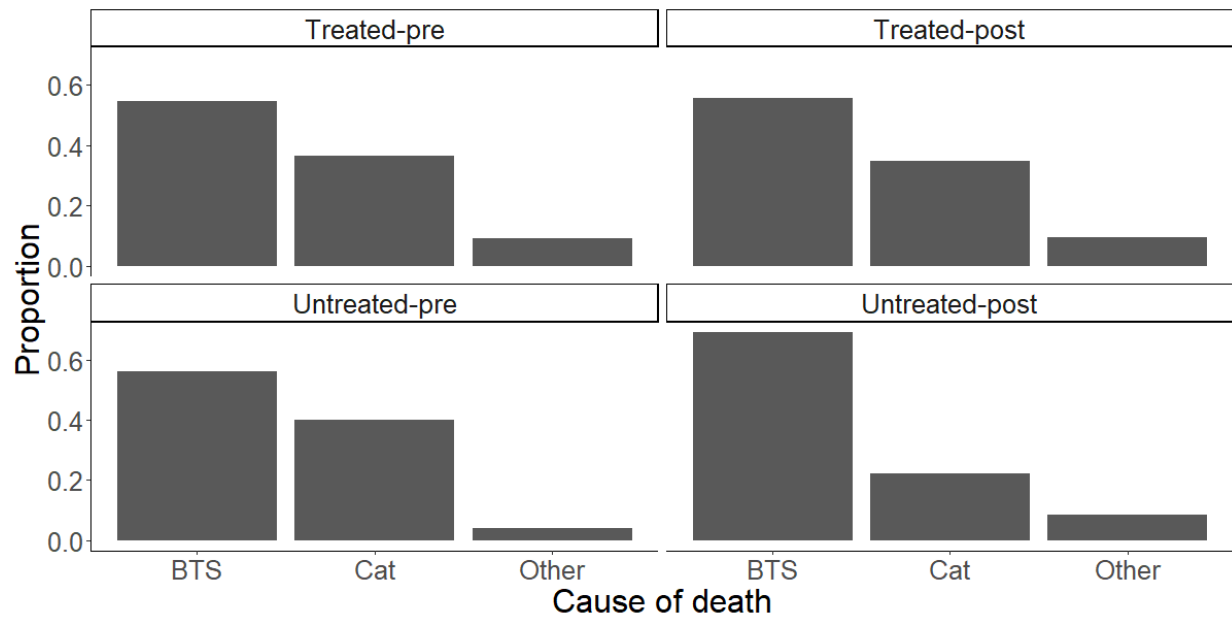


Figure 3: Causes of Sáli (*Aplonis opaca*) fledgling mortality by location (treated vs. untreated areas) and phase (pre-treatment vs. post-treatment), shown by proportion per treatment phase. Mortality causes recorded include Brown Treesnake (*Boiga irregularis*), domestic or feral cat (*Felis catus*), and other causes (e.g. starvation, entanglement, roadstrike, unknown causes).

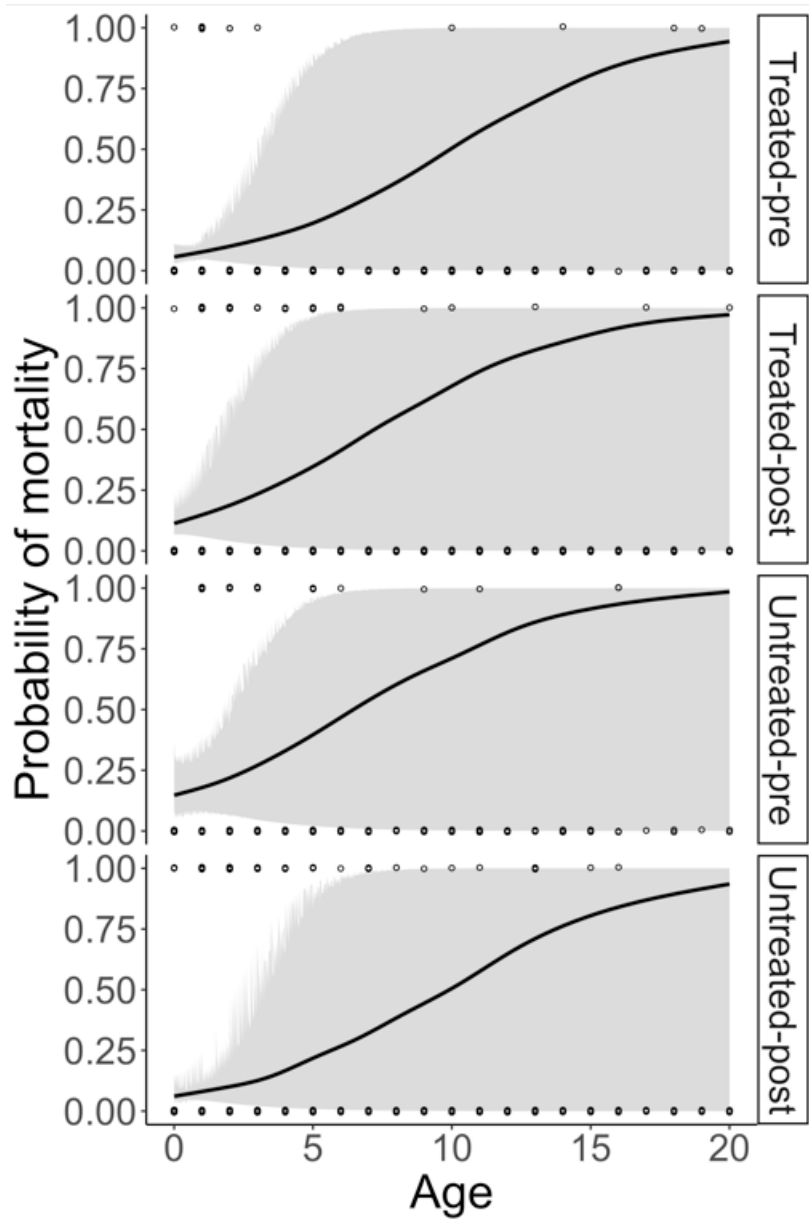


Figure 4: Predicted cumulative probability of daily survival for Sâli fledglings in treated and untreated areas on AAFB, pre- and post-BTS-control.

4.8 Tables

Table 1: Fixed effects table for the survival analysis (formulation: $M2 \leftarrow \text{glmmTMB}(\text{daily} \sim \text{fTreat_phase} + \text{cpue} + \text{age} + (1|\text{fClutchID}), \text{family} = \text{binomial})$).

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	-3.02	0.40	-7.50	<0.001
Treatment-phase: treated, post-control	0.34	0.40	0.85	0.39
Treatment-phase: untreated, pre-control	0.70	0.43	1.63	0.10
Treatment-phase: untreated, post-control	0.85	0.39	2.19	0.03
Catch-per-unit-effort	0.88	0.47	1.89	0.06
Age	-0.09	0.02	-3.98	<0.001

Table 2: Fixed effects table for the cause of mortality analysis (M1: formulation: $M1 \sim \text{glmmTMB}(f\text{Cod_binom2} \sim f\text{Treat_phase} * \text{cpue} + \text{age} + (1|f\text{ClutchID}), \text{family} = \text{binomial})$).

	Estimate	SE	<i>z</i>	<i>p</i>
Intercept	-4.66	0.59	-7.94	<0.001
Treatment-phase: treated, pre-control	0.07	1.05	0.07	0.95
Treatment-phase: untreated, post-control	1.97	0.60	3.27	0.001
Treatment-phase: untreated, pre-control	0.79	0.81	0.98	0.33
Catch-per-unit-effort (CPUE)	6.03	1.72	3.51	<0.001
Age	-0.08	0.03	-2.95	0.003
Treatment-phase: treated, pre-control * CPUE interaction	-1.27	3.81	-0.33	0.74
Treatment-phase: untreated, post-control * CPUE interaction	-5.20	1.84	-2.82	0.005
Treatment-phase: untreated, pre-control * CPUE interaction	-2.74	2.26	-1.21	0.23

Conclusions

In Chapter 1, I found that nearly half of the ingestion attempts by snakes on fledgling Sâli were unsuccessful. There was no difference in the probability of ingestion success across the size range of Sâli fledglings, although this result might not be expected to hold against a broader gradient of prey sizes. The snakes that successfully consumed fledglings were amongst the largest snakes in the population, and the smallest snakes to successfully fledglings appeared to be pushing the absolute limits in terms of the size of prey they could conceivably consume. The most abundant size class of BTS on the landscape were snakes just smaller than those successfully ingesting Sâli. These are snakes large enough to be attracted to birds and other endothermic prey, and all evidence suggests that they are the snakes responsible for the large number of unsuccessful ingestion attempts we recorded at our site. Notably, I did not find any instances where an unsuccessful ingestion attempt caused the mortality of a snake. It has previously been proposed that if prey are valuable enough, and attempts are “cheap” (i.e. not energetically costly), then failed predation attempts are likely to be commonplace. This appears to be the case in our system, and it is likely that future research in other settings will uncover other examples of high rates of unsuccessful ingestion by snakes or other gape-limited predators

In Chapter 2, I uncovered an apparent trade-off in nest-site selection between breeding potential and fledgling survival. Sâli nest sites closer to the forest had greater numbers of yearly nesting attempts, but lower fledgling survival rates, than those farther from forest. Clutch size, nest success, and nestling condition was equal between sites. I suggest that distance from forest confers an energetic cost to Sâli, because they forage almost exclusively in the forest and must commute repeatedly into the forest throughout the day during the nesting period. Therefore, the energetic advantages of nesting closer to forest may allow Sâli to regain condition more quickly and breed more frequently. However, fledglings from nest sites closer to forest are at greater predation risk from BTS, which occur at their high densities in forest and are nearly or fully from the most isolated areas of the urban interior. These selective forces are acting in opposite directions for Sâli pairs, and it is likely that an area of optimal fitness exists at

medium distances to forest. It is probable that other species that have been pushed into marginal habitat by invasive species or other threats face similar life-history trade-offs whereby their areas of highest productivity coincide with high mortality.

In Chapter 3, I found that the survival of fledgling Sâli did not change as a result of a concerted attempt at BTS control in several plots throughout their main remnant breeding range on Guam. Furthermore, the rate of BTS-caused deaths did not decrease as a result of the control effort. While the control effort did evidently remove snakes from the treated areas, it was not possible to assess whether the decrease in density was substantial due to the logistical difficulties associated with monitoring BTS abundance. Nevertheless, BTS remained the leading cause of fledgling deaths in treated and untreated areas, both before the control period and while control measures were being applied. I identified a number of factors that may have dampened the effectiveness of the control efforts at our site: the control areas were relatively small and inevitably subject to reinvasion pressure; an important portion of the snake population was likely too large to be vulnerable to the toxin used; and the abundance of live prey at the site may have counteracted the attractiveness of the bait and lures. These results suggest that in future BTS control efforts, it may be desirable to treat larger areas with lesser edge-to-interior ratios, and with ideally natural or artificial barriers in place to prevent reinvasion. It may be worthwhile to trial deploying control tools in concert, and if possible, to integrate visual surveys into the control matrix, as the tool with the least bias for both removing snakes of all sizes and monitoring their density on the landscape. Efforts should also be made to develop tools with a high level of attractiveness to BTS, and particularly those in a prey-rich landscape.

Taken together, the results of this body of work highlight the importance of striving to achieve a detailed understanding of predator-prey interactions, and using the best available methods to realize that aim. The finding from the first chapter, that BTS kill nearly twice as many Sâli fledglings as they consume, will undoubtedly come as a surprise to many, and would not have been possible with traditional methods for assessing snake diets. Likewise, the conclusions regarding the influence of distance to forest on Sâli

recruitment would have been vastly different had I not monitored the survival of the fledging stage, a life stage that continues to be overlooked in many avian studies. The results of my final chapter, although disappointing, nevertheless represent an important step forward in the management of BTS on Guam. That bait tubes and traps, which have been mainstays of BTS control for decades, are not sufficient to improve Sâli fledgling survival is important new information and suggest that innovation is needed in order to effectively manage BTS in landscapes inhabited by native birds. In Guam, as elsewhere, it will be necessary to continue to defy easy assumption and rigorously engage in the process of scientific enquiry in order to achieve much-needed conservation gains.

5.1 Management and conservation implications

In Chapter 1, I found that nearly half of the Sâli mortalities caused by BTS were unsuccessful ingestion events. Together with our morphological data on Sâli and BTS, we concluded that the unsuccessful ingestion events are most likely caused by snakes that are too small to successfully consume the birds. This finding entails that that relatively small snakes pose a significant predation risk to birds on Guam. Broadly speaking, the major implication of this result from a management perspective is that the size range of snakes that need to be targeted for avian conservation on Guam has been widened. “Sliming” snakes, along with snakes capable of ingesting birds, must be removed from a given conservation site for the predation threat from BTS to be eliminated. Because snake control tools are all size-specific, this finding may have implications in terms of tool selection. While it is likely that most or all “slimers” can be targeted with tools that employ ectothermic baits and lures (at sites where such tools are effective), BTS control using visual searches is preferable because it targets all snake size classes. Removing the smallest snakes at a site (which are not targeted using traps or toxic bait) is advantageous because it eliminates the risk from individuals that are on the cusp of becoming potential “slimers”. Note that the range of snake sizes that pose a risk of unsuccessful ingestion to birds is dependent on the size of the bird species: small birds like sparrows or white-eyes will have a very narrow range of potential “slimers”,

while large species like crows will have a broad range. Managers of species of conservation concern threatened by invasive or native snakes in other systems should consider the predation risk posed by relatively small snakes to their focal species.

In Chapter 2, I describe a trade-off in nest-site selection for Sâli between a measure of their fecundity (the number of yearly nesting attempts) and their probability of fledgling survival. The distance of nest sites to forest is a proxy for both factors, with the number of yearly nesting attempts decreasing and the probability of fledgling survival increasing along with the distance of nest sites to forest. Importantly, the latter relationship appears to be mediated by BTS predation risk: the probability of BTS predation decreases with increasing distance to forest (higher probability of BTS predation closer to the forest edge). Further analysis is needed in order to understand the relationship between distance to forest and overall Sâli fitness. Is there an optimal middle ground in terms of distance to forest, whereby the number of yearly nesting attempts and fledgling survival are balanced, or is the highest expected fitness at an extreme of the range (e.g. in the urban interior, where fledgling survival is highest)? There will be important management implications from these findings. For example, it will be possible to inform managers of the ideal distance to forest range within which to install nest boxes, as well as areas to avoid where Sâli fitness would be expected to be negative (possible ecological traps). If effective BTS control is implemented, then Sâli fledgling survival would be expected to increase in areas closer to the forest edge. Moreover, the zone of optimal fitness may shift, and Sâli population growth will likely accelerate. It is probable that similar trade-offs between fecundity and survival exist for other species relegated to suboptimal habitat, and in particular those threatened by invasive predators. Managers should aim to identify such cases using comparable methodology, which would allow them to identify habitat where recruitment can be improved if threats to survival are reduced.

In Chapter 3, I found that Sâli fledgling survival did not respond to a BTS control effort within their remnant range on Guam. While it could be suggested that Sâli fledgling survival is not sensitive to the presence of BTS, in fact BTS continued to predate fledglings at a high rate throughout all phases of the

experiment. It appears that the control measures implemented were not sufficient to reduce the predation threat posed by BTS at the site. While a discouraging result, these findings are nevertheless informative from a management perspective. Methodological changes will be required in future BTS control attempts if an increase in avian recruitment is the goal. There are many avenues for improvement to the experimental design: the treatment areas could be made larger, entailing a lower edge-to-interior ratio; they could have more substantial barriers to BTS movement along their borders, such as multi-lane roads; the control tools could be implemented in concert, rather than in sequence; and the acetaminophen dose in the toxic bait could be increased (regulations permitting) to account for the high proportion of large snakes at the site. Perhaps most importantly, implementing a method for monitoring changes in BTS density into the protocols would offer crucial feedback on the effectiveness of control measures. Using visual searches as part of the control program may offer a win-win solution, because they offer not only the tool that targets the broadest range of snake sizes, but also the one that provides the most sensitive index to changes in BTS density. My results should serve as a cautionary example for managers that the outcome of invasive predator control measures must not be taken for granted. The effectiveness of a control program should be rigorously assessed both in terms of its effectiveness in reducing predator density and also in terms of improving native species survival.

While my dissertation research focused primarily on the relationship between Sâli and BTS, I found that cats continue to pose a threat to Sâli survival, accounting for approximately a third of mortalities. Implementing cat control measures may offer a relatively straightforward approach for managers to improve avian survival on Guam, since guidance on cat control in similar environments is relatively widespread. Moreover, implementing cat control ahead of BTS suppression would anticipate any compensatory increases in cat predation once BTS densities are reduced.

5.2 Next steps in research

One of the most enticing prospects as a researcher is the thought of conducting a follow-up project. Without fail, working on one question seems to bring about a multitude of other question for yourself or others to tackle (at some indeterminate future time). This dissertation work was no exception to that rule. In my first chapter, I found that nearly half of the Sáli fledglings killed by BTS were not actually swallowed by the snakes. While all the circumstantial evidence suggested that relatively small snakes are responsible for most or all of the unsuccessful ingestion attempts, my methods did not allow me to actually measure the snakes responsible. Therefore, a logical follow-up question is: what sizes of snakes are “sliming” their prey? A pair of colleagues (Shane Siers and Bruce Jayne) have conducted a study investigating this question using captive snakes and dead prey; tackling this question in the field would require impressive innovation given the technical challenges involved. Some other low-hanging fruit: how often does sliming happen in other systems? Under what circumstances does it become prominent? How does the rate change as snakes of a given size are removed from the system, or as prey availability changes?

In my second chapter, I proposed that a trade-off exists in Sáli nest-site selection between the proximity to foraging areas (allowing more frequent nesting attempts) and the risk of fledgling predation. The distance of nest sites to forest was used as a proxy for both factors selection forces. While the evidence available suggests that such a trade-off is possible, the logical alternative is that more frequent nesting at nest sites closer to the forest edge is simply a byproduct of higher rates of predation. An experimental approach could neatly solve this debate: for example, by providing supplementary food to Sáli pairs in the urban interior, it could be determined if the energetic advantage of reduced commutes allows them to breed more frequently. It may be possible to model the energetics of the parental commutes by Sáli, in order to gain further insight into how costly the longer commutes are for pairs at nest sites farther from forest. Alternatively, and perhaps more controversially, fledgling survival could be manipulated in order to provide greater clarity (e.g. fledglings removed at sites farther from forest). An ideal approach would be to monitor how breeding frequency changes if and when BTS and cat are removed from the system,

allowing improved survival of fledglings. In the interim, studying Sâli reproduction on other islands with lower predation rates may provide some insights.

In my third chapter, I reported on Sâli fledgling survival during an experiment to reduce BTS densities. The unfortunate conclusion of that work was that fledgling survival did not improve as a result of the BTS control attempt, and the rate of snake predation did not change. There are countless glaring next steps to this work, most revolving around the central question: how can BTS control be made effective in this environment? A number of possible factors to change are listed above in section 5.1, and I will not repeat them here. Instead, I will propose a different approach to conducting BTS control involving community participation and citizen science. One of the frequently-cited criticisms of using visual searches as a control tool is the amount of labor involved. By integrating community volunteers into the team, costs could be reduced, all the while fostering a sense of stewardship in participants. A collaborator and I founded such an effort in parallel to my dissertation work, and the results have been highly encouraging (Kastner & Terral 2023). It would be heartening to see such efforts replicated across Guam, catalyzing the restoration of the island's ecosystems through the collective participation of its community.

5.3 Bibliography

Kastner, M., & Terral, O. (2023). Establishing a Volunteer Group to Assist in the Eradication of Invasive Brown Treesnakes from Islan Dâno'(Cocos Island), Guam. *Human–Wildlife Interactions*, 17(2), 11.