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ARTICLE

Predation thresholds for reintroduction of native avifauna following suppression of invasive Brown Treesnakes on Guam

Robert M. McElderry^{1,2}  | Eben H. Paxton³ | Andre V. Nguyen³ | Shane R. Siers⁴

¹Research Corporation of the University of Guam, Mangilao, Guam, USA

²Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

³U.S. Geological Survey Pacific Island Ecosystems Research Center, Hawaii National Park, Hawaii, USA

⁴U.S. Department of Agriculture APHIS, Wildlife Services, National Wildlife Research Center, Barrigada, Guam, USA

Correspondence

Robert M. McElderry
Email: mcelderryr@triton.uog.edu

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Abstract

The brown treesnake (BTS) (*Boiga irregularis*) invasion on Guåhan (in English, Guam) led to the extirpation of nearly all native forest birds. In recent years, methods have been developed to reduce BTS abundance on a landscape scale. To help assess the prospects for the successful reintroduction of native birds to Guåhan following BTS suppression, we modeled bird population persistence based on their life history characteristics and relative sensitivity to BTS predation. We constructed individual-based models and simulated BTS predation in hypothetical founding populations for each of seven candidate bird species. We represented BTS predation risk in two steps: risk of being encountered and risk of mortality if encountered. We link encounter risk from the bird's perspective to snake contact rates at camera traps with live animal lures, the most direct practical means of estimating BTS predation risk. Our simulations support the well-documented fact that Guåhan's birds cannot persist with an uncontrolled population of BTS but do indicate that bird persistence in Guåhan's forests is possible with suppression short of total eradication. We estimate threshold BTS contact rates would need to be below 0.0002–0.0006 snake contacts per bird per night for these birds to persist on the landscape, which translates to an annual encounter probability of 0.07–0.20. We simulated the effects of snake-proof nest boxes for Sihek (*Todiramphus cinnamominus*) and Sâli (*Aplonis opaca*), but the benefits were small relative to the overall variation in contact rate thresholds among species. This variation among focal bird species in sustainable predation levels can be used to prioritize species for reintroduction in a BTS-suppressed landscape, but variation among these species is narrow relative to the required reduction from current BTS levels, which may be four orders of magnitude higher (>0.18). Our modeling indicates that the required predation thresholds may need to be lower than have yet been demonstrated with current BTS

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management. Our predation threshold metric provides an important management tool to help estimate target BTS suppression levels that can be used to determine when bird reintroduction campaigns might begin and serves as a model for other systems to match predator control with reintroduction efforts.

KEYWORDS

Aplonis opaca, *Boiga irregularis*, *Corvus kubaryi*, *Hypotaenidia owstoni*, Island endemic avifauna, Mariana Islands, nonnative predators, Pacific Islands conservation, *Ptilinopus roseicapilla*, reintroduction, *Rhipidura rufifrons*, *Todiramphus cinnamominus*

INTRODUCTION

The threat posed by nonnative predators to island-endemic avifauna is of global importance. Islands support 19% of global avifauna diversity but comprise only 5.3% of Earth's land area, while 95% of avifauna extinctions and 58% of critically endangered birds globally are from islands (Tershy et al., 2015). Introduced predators on islands have proven more detrimental to species persistence than other serious threats, such as fragmentation, deforestation, and climate change (Clavero et al., 2009; Doherty et al., 2016; Nogales et al., 2013; Russell et al., 2016). Controlling invasive predators on islands may be one of the most effective global conservation strategies given the potential biodiversity returns (Doherty et al., 2016).

Globally, several attempts at island-wide eradication of nonnative predators have been made to prevent extinctions and restore biodiversity. These eradication campaigns have been successful in several instances (e.g., Clout & Russell, 2006; Howald et al., 2007; Nogales et al., 2004) and in many cases have allowed the reestablishment of native species (e.g., Atkinson, 2001; Jones et al., 2016). However, many predators cannot be fully eradicated using existing techniques, in which case managers are left with difficult choices (Baxter et al., 2008; Green & Grosholz, 2021). Simply accepting the new ecosystem state may allow for continued declines and extinction of native species and runs counter to legal requirements, such as the Endangered Species Act in the United States or the Bird and Habitat Directives in the European Union. Alternatively, when the eradication of predators is not possible, the best conservation approach may be long-term suppression to levels sufficient to allow reestablishment of prey populations (Sinclair et al., 1998). The term functional eradication has been applied to describe the suppression of invader populations below levels that cause unacceptable ecological effects (Green & Grosholz, 2021). However, determining what level of suppression is necessary to achieve functional eradication is subject to many unknowns

(Moseby et al., 2011), and embarking on a suppression campaign with no predefined end point is undesirable (e.g., Davidson & Stone, 1989). Other options include preserving species on neighboring predator-free islands or establishing captive populations (MAC Working Group, 2014). The use of neighboring islands has been an important conservation tool in many places (Saunders & Norton, 2001) and can be a source of individuals for future reintroductions, but appropriate islands do not always exist. Captive breeding programs are often then the last option, but they are costly and may be subject to issues such as inbreeding depression, disease outbreaks, and long-term behavioral changes (Trask et al., 2020, 2021). Reintroducing species into their historical range where nonnative predators remain would benefit from identifying predator threshold levels below which reintroduction efforts have high probabilities of success.

One of the best examples of an invasive predator decimating a native biological community is the brown treesnake (BTS) (*Boiga irregularis*) on the island of Guåhan. Accidentally transported to Guåhan following World War II, the BTS spread to occupy the entire island by the early 1980s (Rodda et al., 1992; Savidge, 1987). This generalist arboreal predator caused or contributed to the extinction or extirpation of most of Guåhan's native avifauna (Rodda & Savidge, 2007; Wiles et al., 2003). Despite decades of research and tool development (summarized in Clark et al., 2018), island-wide eradication of BTS from Guåhan appears to be out of reach in the near future. However, the recent development of a new automated system for the production and aerial delivery of toxic baits may allow significant suppression of BTS abundance on a landscape scale (Siers et al., 2019; Siers, Shiels, & Barnhart, 2020). To date, the short-term effects of this baiting system have been evaluated within a 5-ha BTS enclosure/exclosure (Nafus et al., 2022) and a 55-ha BTS enclosure (Siers, Eisemann, et al., 2020) demonstrating that snake suppression is readily achievable in a finite area but that eradication is difficult. Meanwhile, many agencies and interest groups are committed to reestablishing components of Guåhan's native avifauna

through the reintroduction of captive-reared birds or translocation from other islands in the Marianas if BTS can be eliminated or sufficiently suppressed within protected areas (Brock & Beauprez, 2000; Haig et al., 1990; MAC Working Group, 2014; Trask et al., 2021). Guåhan may soon reach a point where suppression at a local level allows for the reintroduction of some of Guåhan's extirpated bird species. A logical precursor to this step is the construction of models that estimate the probability of success given variable estimates of BTS predation risk and a means of quantifying uncertainty in the probability of success that can be used for the planning and development of a comprehensive refaunation strategy.

In this study, we developed models to identify predation thresholds below which it may be possible to reestablish native bird species on the island of Guåhan in the presence of BTS at suppressed levels. Identifying approximate BTS densities that can be tolerated by bird populations is complicated by the difficulty of obtaining reliable and precise estimates of BTS density at any given time and place. Current methods for BTS density estimation are either biased or imprecise, owing to very low detectability and model assumption violations, or are too costly for practical application (Amburgey et al., 2021; Christy et al., 2010; Rodda & Campbell, 2002; Tyrrell et al., 2009). However, it is not simply the number of snakes on the landscape that matters for bird survival; it is the frequency at which birds are killed by BTS (and other causes of mortality). Frequency of predation depends on encounter rates and susceptibility to predation given an encounter, which is dependent on several factors, including overall snake density, snake and prey species' size, behavior, and habitat use. If we assume that suppression will maintain a constant BTS attack rate, then determining the level of suppression that promotes population persistence for birds depends in part on both a bird's traits and its population dynamics. Individually, birds that effectively avoid or reliably survive encounters with BTS are less vulnerable. Collectively, species with high reproduction rates that have potential growth rates higher than the rate at which birds are consumed are also less vulnerable. Having either higher survival odds or higher reproduction rates may allow a particular bird species to become established and persist in BTS-suppressed areas, but we cannot directly measure these characteristics in situ given the absence of Guåhan's avifauna. To bridge this knowledge gap, knowledge from a panel of experienced Guåhan bird and BTS biologists was elicited to predict the outcomes of individual bird–snake encounters (McElderry et al., 2021). Consensus indicated notable differences among bird species and life stages in their vulnerability to BTS, especially

body size and a few other physical and behavioral attributes that were likely important for determining species-specific rates of predation by BTS.

To quantify BTS predation thresholds specific to different bird species, we developed models to link individual species' vulnerabilities and demographic rates (e.g., reproduction and survival rate) within a life cycle and projected the resulting population dynamics for each of our seven focal species to predict how different BTS predation levels would affect bird population dynamics and probability of persistence. Specifically, we pursued the following objectives: (i) We developed population viability models for each bird species. (ii) We defined a direct link between BTS live-lure contact rates and potential impact on bird populations from BTS encounters and predation. (iii) We evaluated the level of tolerable BTS predation rates for each bird species and ranked species by their likelihood of persistence at an achievable level of BTS predation threat. (iv) We explored aspects of BTS management that might influence reestablishment success.

Although expert knowledge can provide insights into main factors that affect prey vulnerability (McElderry et al., 2021), population models evaluate interactions of multiple factors, providing a synergistic assessment of vulnerability over all life stages and allows for sensitivity analysis, such as the sensitivity of population growth to changes in each demographic rate that is affected by BTS. Highly sensitive species will respond more strongly to different levels of BTS suppression. Considering the dearth of knowledge in this system, sensitivity analysis also serves as a means for quantifying uncertainties, thereby highlighting areas for continued research and providing managers with a confidence range in the results. Altogether, the work we describe in what follows illustrates how we can integrate available information to bridge knowledge gaps, quantify suppression thresholds for nonnative predators, and evaluate the potential for success in reestablishing native fauna when there is a lack of direct information.

METHODS AND MATERIALS

Study system

Nearly all avifauna once native to Guåhan—especially those utilizing forest habitats—declined in response to the introduction and spread of BTS, and most went extinct or were extirpated from Guåhan over several decades (Wiles et al., 2003). In advance of this rapid decline, birds of some species were captured, and captive breeding programs were initiated with the ultimate goal

of releasing birds back into the forests of Guåhan (USFWS, 1990); other birds persist on other islands in the Commonwealth of the Northern Mariana Islands (CNMI) (Sankattan Siha Na Islas Mariånas) and are candidates for translocation to Guåhan following BTS suppression. We selected seven birds for our study that might be considered candidates for release on Guåhan in the future, referring to them by their local Chamorro name: Ko'ko' (Guam rail) *Gallirallus owstoni*, Åga (Mariana crow) *Corvus kubaryi*, Totot (Mariana fruit dove) *Ptilinopus roseicapilla*, Sâli (Micronesian starling) *Aplonis opaca*, Sihek (Guam kingfisher) *Todiramphus cinnamominus*, Chichirika (Rufous fantail) *Rhipidura rufifrons*, and Nosa' (bridled white-eye) *Zosterops conspicillatus*. We list these species in order of decreasing body size (Table 1), an important indicator of predation risk (McElderry et al., 2021), with Ko'ko' almost 30 times heavier than Nosa'.

Three of these birds are currently being reared in captivity and are top candidate species for release into the wild. From a captive population, colonies of Ko'ko' have been successfully established on Cocos Island, just offshore Guåhan (Pitt et al., 2012), and on Luta (Rota) Island north of Guåhan (Beauprez & Brock, 1999a; Witteman et al., 1990). Sihek currently exists only in captivity within a network of zoos, but conservation plans are under way to establish populations on small snake-free islands outside of the species' historical range (Trask et al., 2020). Concerns for the viability of Åga on Luta, where it still persists in the wild, have led to captive rearing of Åga for release on Luta, and the Mariana Crow

Recovery Team has also considered translocating Åga to other Northern Manislan Mariånas (John Morton, Mariana Crow Recovery Team, written communication, 2021). Conspecifics of the Totot, Chichirika, and Nosa' occur naturally elsewhere in Manislan Mariånas, but the risk of invasion by BTS on these other islands represents a real and ongoing threat to species across the island chain (MAC Working Group, 2014). In response, these birds and others have been translocated to unoccupied islands in the CNMI to increase the number of islands where they occur (MAC Working Group, 2014; Radley, 2014). Aside from the cave-dwelling Yayaguak (Mariana swiftlet) *Aerodramus bartschi*, Sâli is the only native forest bird that remains on Guåhan, restricted to urban habitats where reduced snake levels and anthropogenic landscapes allow it to persist (Pollock et al., 2021; Savidge et al., 2018).

All of these birds have primarily used forest habitats on Guåhan except Ko'ko', a flightless bird that prefers scrub and woodland habitat with low cover, where it forages for plant and animal food items (Jenkins, 1979). Conversely, Totot is a forest-dependent species that occupies the mid to upper canopy, where it feeds on fruit (Craig, 1996). More gregarious than the relatively solitary Totot, Åga was also reported to prefer mature forest (Jenkins, 1983). However, Åga was frequently observed in a broad array of habitats on Guåhan, which may be explained by its broad omnivorous diet (Jenkins, 1983). Sihek is a notably active predatory bird that has been observed in the wild hunting prey on the ground from perches above (Jenkins, 1983). Both Sâli and Sihek are

TABLE 1 Demographic characteristics used in our models for our focal bird species.

Demographic characteristic	Nosa' ^a	Chichirika ^b	Sihek ^c	Sâli ^d	Totot ^e	Åga ^f	Ko'ko' ^g
Adult mass (g)	7.7	8.05	63.25	82.8	84.8	249	227
Hatching year survival	0.47	0.36	0.37	0.43	0.481	0.638	0.41
Adult survival (annual)	0.61	0.57	0.78	0.71	0.85	0.904	0.82
Age of maturity (years)	10 months	10 months	1	1	1	2	1
Age of senescence (years)	9	9	13	9	17	15	13
Pair bonding rate	1	1	0.6	1	1	1	0.36
Clutch size (no. eggs)	2–3	2	1–3	2	1	1–4	3–5
Nest success	0.31	0.51	0.82	0.5	0.3	0.257	0.53
Fledglings per clutch	1.67	1.84	1.30	1.81	1	1.25	1.96

Note: Some metrics were not available for our focal bird species, so we used metrics from close relatives.

^aAmidon (2000), Brook and Kikkawa (1998), Kikkawa and Wilson (1983), MAC Working Group (2008), Radley et al. (2011), Sachtleben (2005), Yamashina (1932).

^bJenkins (1983), Nietmann (2018), Nietmann and Ha (2018), Radley et al. (2011), Saracco et al. (2014), Wiles et al. (2003).

^cBahner et al. (1998), Blackwell and Andrews (2019), Kesler (2005), Kesler and Haig (2007), Pyle et al. (2018).

^dBaker (1951), Craig and Feare (2020), Hartert (1898), Pollock et al. (2019), Pyle et al. (2008, 2018), Radley et al. (2011), Savidge et al. (2018).

^eBlackwell & Andrews (2019), Che-Castaldo et al. (2019), Claridge (1987), MAC Working Group (2014), Villagomez (1987).

^fBaker (1951), Faegre et al. (2021), Ha et al. (2010), Morton et al. (1999), National Research Council (1997), Zarones et al. (2015).

^gBeauprez and Brock (1999a, 1999b), Beauchamp et al. (2009), Jenkins (1979), Haig et al. (1990).

cavity nesters, but while Sihek excavates termite nests in forested habitat (Kesler, 2002; Kesler & Haig, 2005), Sáli has taken to the urban environment, where it nests in a variety of artificial cavities (Savidge et al., 2018). Historically, the omnivorous Sáli was a habitat generalist on Guáhan but now forages in forests near urban areas only during the day (Pollock et al., 2021). Both Chichirika and Nosa' may have once preferred mature forests, but seem to have taken well to more invaded woodland and secondary growth forests (Craig, 1996; Jenkins, 1983), where they feed primarily on insects (Jenkins, 1983; MAC Working Group, 2008). We selected these species both to include priority species for conservation actions and to represent a range of body sizes and life histories. The diversity of species allows us to explore the range of characteristics that could influence the success of reintroduction given varying BTS predation levels, providing guidance for future efforts at reintroduction of the many birds once native to Guáhan.

Model description

Modeling the release of relatively few birds, projecting all possible future fates, and determining whether enough of them can survive BTS predation to establish a breeding population is central to our aim. Matrix projection models are a standard demographic model in biology (Salguero-Gómez et al., 2015, 2016), but the standard projection equation, $N_{t+1} = AN_t$, treats the population vector N_t as a vector of stage class densities each of which grows or shrinks in fractional increments. Although this works well for average demographics in a large population, the average is often not appropriate for small populations, where demographic stochasticity alone may result in extinction despite favorable demographic rates. In such cases, a stochastic modeling approach may be more useful because it can project discrete individuals who may live or die within a small founding population that might persist or go extinct. We included demographic stochasticity by taking an individual-based model (IBM) approach. We first developed matrix projection models for each species to define the mathematics that describe the life cycle of each species (Appendix S1). Then we used these matrix models as scaffolding in developing individual based models that better suited our needs. In doing so, we retained aspects of the standard matrix model approach with which biologists are often familiar while achieving the benefits of IBM flexibility. We constructed each IBM so its projection matched the corresponding matrix projection, but importantly each IBM projection differed due to random chance. The range of projection outcomes therefore estimated a range of

possible outcomes, even though we did not vary demographic rates. Furthermore, the flexibility of the IBM framework facilitated nuanced demographic features, for example, pair bonding, shared fates, and, importantly, individual-level snake–bird interactions.

To set up each IBM, we defined a Markov model (P_X), which in our case is a matrix that contains only survival and stage transition probabilities. As in a matrix model, each column j represents a bird's life stage at time t (states), and each row i represents the life stage in the next time step, $t + 1$. Unlike in a matrix model, P_X includes a death state. Death is an absorbing state, that is, no resurrection. We included several details in P_X that we deemed critical to each bird's life cycle: age of maturity, sex, age of senescence, and breeding stages for females (see Appendix S1 for details). We also selected a relatively short time step (2 months)—a 1-year time step is common but not the rule—to balance our objectives, available data, reproductive biology, and modeling flexibility. At each time step, an individual in state j at time t was randomly placed in state i at time $t + 1$ according to P_X .

Breeding stage dynamics that govern the periodicity of clutch production were built into P_X . We used basic reproductive biology (e.g., nesting time, clutch size, nest success, duration from nesting to fledgling, duration of postfledging parental care, and juvenile development time) to structure and parameterize a breeding model for each species. Depending on each bird's biology, we defined up to four breeding stages—pair bonded and either nonbreeding, breeding, or in parental care or not pair bonded and not breeding—and we crafted three different reproductive mechanisms for our focal species (shown in Figure 1; see also Appendix S1). We defined the non-pair-bonded stage for Ko'ko' and Sihek (Figure 1a) because Ko'ko' is known to forgo breeding in the absence of compatible mates (Fontenot et al., 2006; Witteman et al., 1990), and Sihek exhibits a structured breeding community where “helpers” forgo breeding in the presence of “dominant” breeders (Kesler, 2005; Kesler & Haig, 2007). We used a three-stage breeding model for Ága and Totot (Figure 1b), given their time spent in parental care. We used a two-stage breeding model for Sáli, Chichirika, and Nosa' (Figure 1c), whose juveniles, even with brief parental care, are largely independent in about 2 months (Appendix S1).

For fertility, we generated a whole number of offspring per clutch for each successfully breeding female. To do so, we used a multinomial probability distribution defined by F_X , which was a vector that sums to one and contains the probability of one, two, or n offspring, where n represents the maximum number of fledglings per clutch that a bird species can produce. For models with

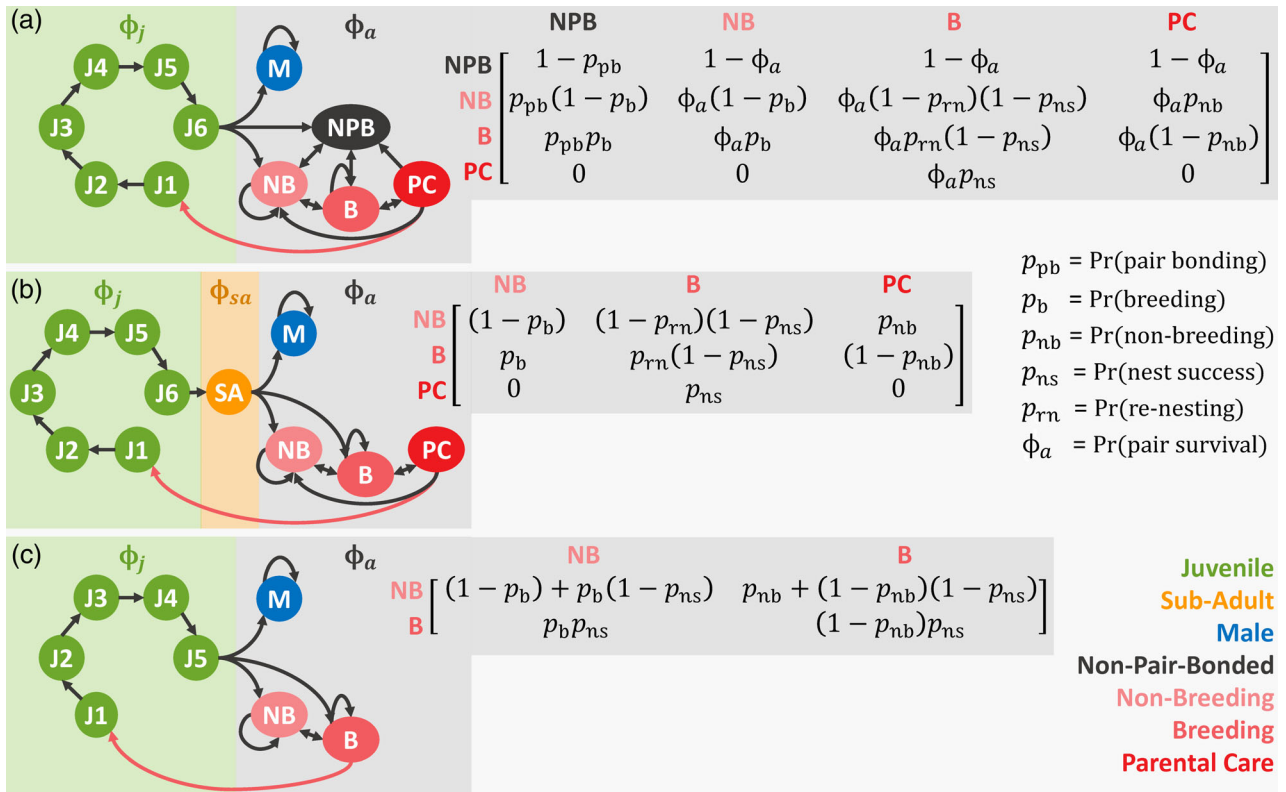


FIGURE 1 Life cycle diagrams showing two of several configurations we used to represent Guáhan avifauna. Juveniles in their first year go through five or six 2-month time steps before adulthood. In life cycle (a), new adults are assigned a sex, and females are either pair bonded or not pair bonded. Only pair-bonded females can progress through three stages of breeding. In life cycle (b), juveniles enter the subadult stage before being assigned a sex. Females in life cycle (b) pass through three breeding stages without regard to pairing. In life cycle (c), females are either breeding or nonbreeding. Here, only those females with nest success enter the breeding stage. Matrices at the right of each life cycle display the transition rules among breeding stages (Appendix S1). All columns sum to one.

parental care, offspring were generated following parental care and were subject to the first juvenile stage survival rate before being added to the second juvenile stage in the following time step.

Demographic rate estimates

We gathered a mixture of demographic, life history, and behavioral information for either our focal species, which, except for Sáli, were either extinct in the wild or extirpated from Guáhan, or close relatives (Table 1) (McElderry et al., 2022).

Survival

We obtained field estimates of annual survival for adults of most focal species and for juveniles of some species (Table 1) (McElderry et al., 2022). In the absence of juvenile survival, we set juvenile survival to half of the annual adult survival rate. We used the sixth root of

annual survival to represent a 2-month survival rate, and because we modeled the effect of BTS predation separately, we used survival estimates without the effects of BTS (reported for Sáli fledglings, Pollock et al., 2019). Similarly, we removed reductions in survival reported for cat predation (but not automobile strikes) for Ko'ko' (Beauprez & Brock, 1999a, 1999b), under the assumption that feral cats would be removed prior to bird release.

Fledged juveniles are particularly vulnerable to predation, but as fledglings mature, their survival rapidly increases to match adult survival. We defined a concave, curvilinear function of 2-month survival rates that started low and reached adult survival at 1 year of development. The cumulative product of this survival function over 1 year matched the annual juvenile survival estimate. We truncated the last value of this function for birds that mature at 10 months of age (Nosa' and Chichirika), and we lengthened it for Ága, which mature at 2 years of age (Faegre et al., 2019), adding 1 year's worth of the adult survival rate reduced by 5% in a subadult stage (Figure 1b and Table 1).

Fecundity

We set reproductive output for each species by defining the number of offspring possible per brood and by modulating the annual frequency of successful breeding attempts. Using published accounts of brood sizes in the wild, we defined each probability distribution for the number of offspring per successful brood, F_x , to match mean fledging rates (Table 1). Nest success rates were available for many of our focal birds, as were the reneating rates following unsuccessful nests (Table 1). Using various reported rates for each species, we considered brood frequency, reneating rates following successful and unsuccessful nests, and mean annual fecundity in selecting breeding probabilities, p_b , p_{rn} , and p_{nb} , which regulated brood frequency, reneating, and recuperation following successful reproduction.

We set the probability of pair bonding equal to 1.0 for all birds except for Ko'ko' and Sihek ($p_{pb} = 0.364$ and 0.6, respectively). For Ko'ko' we used the mean pair bonding rate reported for the Weka rail (*Gallirallus australis*; from 0.12 to 0.78; SE = 0.079; Beauchamp et al., 2009), and for Sihek we used the probability of advancing from helper to dominant status (Kesler & Haig, 2007).

Fine-tuning

We tuned our parameter estimates for congruence between each respective matrix model and IBM and to generate realistic output. For example, the number of broods per year was not a parameter in any model, but we tweaked several breeding stage transition parameters until mean model projections matched brood frequency targets (see R scripts in McElderry et al., 2022). We narrowed these to a few unknown demographic rates for each bird and then searched for the parameter combination that optimized congruence with target demographic metrics that emerged from model projections.

We calculated the intrinsic rate of population growth, λ —a crucial indicator for potential reestablishment success—both as the dominant eigenvalue of each projection matrix (Caswell, 2001) and as the relative growth rate using population time series from our simulated population trajectories in each IBM (Morris & Doak, 2002). When tuning our models, we targeted relatively low intrinsic growth rates, that is, $\lambda = 1.10 \pm 0.05$. Although some growth rates have been reported either in the wild or in captivity for our species, we ultimately could not know exactly how quickly any of these birds would multiply if released on Guåhan, but the demography of some birds simply generated more rapid population growth than others. However, when we analyzed the sensitivity

of our results to the assumed population growth rate, we simply recovered the vulnerability rankings reported by McElderry et al. (2021).

Predation by BTS

Rather than a tight predator–prey dynamic whereby the abundances of each competitor covary, we focused on the unilateral effect of predators on prey. The fact that BTS persists at high densities without birds on Guåhan strongly indicates some independence of BTS population dynamics from bird abundance. Furthermore, we focused exclusively on a scenario in which BTS will be actively suppressed at or below a threshold encounter rate. We treated threshold BTS encounter rates as an unknown variable, and we simulated a sequence of increasing rate levels to estimate the effect on the viability of each bird species. We defined predation as a two-step process involving the probability of a bird being encountered by a BTS and the probability of death in the event of an encounter.

BTS encounter rates

Contact rates at live lure camera traps is our best means for measuring the relative abundance of this elusive, nocturnal treesnake (Siers, 2021; Yackel Adams et al., 2019). Although translating contact rates to actual abundance is subject to many assumptions and unknowns (Amburgey et al., 2021), contact rates quite literally represent the rate at which a prey item might be expected to be encountered by a foraging snake. Thus, we used contact rates (snake contacts per lure per night) as a direct measure of a background predator–prey contact rate, and we assumed that this sufficiently sidestepped problem variables that would be important in determining encounter rates—for example, abundance, size distribution, foraging patterns, and satiation rates—for which we lacked good measurements.

Each bird's behavior will differentially affect its chance of a BTS encounter. To match the time step in our models, we first scaled up nightly contact rates to the probability of at least one encounter within a 2-month period (Appendix S1). We then defined a range of baseline BTS encounter probabilities for our simulations and used the results from a survey of experts (McElderry et al., 2021) to convert baseline to species-specific encounter rates.

The BTS is presumed to threaten both the individual initially encountered and other birds nearby (McElderry et al., 2021; Savidge, 1987). In all models, eggs, nestlings,

and dependent juveniles in parental care were at risk of secondary encounter if their mother was encountered. Juveniles were considered dependent only during the first 2 months after leaving the nest. For adult partners, we simulated one of two alternative scenarios. Either each adult was at risk of being encountered by a BTS, independently of other birds, or its chance of encounter was linked to its partner's. In this latter scenario, pairs were assumed to always roost together. One adult was identified as the primary contact (using an even probability) and classified as encountered, whereas the other adult was treated as a secondary contact at risk of secondary encounter similar to all nestlings and juveniles in parental care. Only bonded pairs were encountered together, whereas single adults and independent juveniles were always encountered individually. To allow each secondary contact a chance at evasion, we set probabilities for secondary encounters using stage and species-specific estimates from our survey (McElderry et al., 2021). In the event that eggs, nestlings, or dependent juveniles survived a BTS encountered but neither parent did, we did not allow these young to survive.

Fate following BTS encounter

The mortality of an encountered bird varied substantially among our focal species and among life stages (McElderry et al., 2021). Overall, smaller birds had higher mortality rates than larger birds, and earlier developmental stages within each bird species and birds on a nest had higher mortality rates than adults (McElderry et al., 2021). We used these values elicited from experts in simulations and note that experts assumed an average-sized mature BTS (1050- to 1200-mm snout-to-vent length [SVL]) in determining mortality rates.

Simulations to estimate range of uncertainty

We explored uncertainty in predation risk by simulating various levels of encounter risk, mortality risk on encounter, and whether or not a pair-bonded adult was also at risk when its partner was encountered. We defined a gradient in encounter risk from zero to a rate beyond which all species were projected to decline (McElderry et al., 2022). For mortality risk on encounter, we defined a gradient that spanned all values reported for the life stages of all species (McElderry et al., 2021). We simulated all combinations of these gradients for each individual and pair-bond risk type, and we calculated the mean annual rate of population growth for each

bird species over 200 random populations initiated by 50 founding adults and projected 20 years into the future (30 or 40 years for demographic summaries). For Sáli and Sihek, we defined additional model scenarios that mimicked the distribution of nest boxes in BTS suppressed forests by reducing bird-on-nest encounter rates and secondary encounter risk for nestlings. Overall, these simulations revealed the range of uncertainty in this system.

We set up a simulation scenario to imitate Sáli on Andersen Air Force Base (AAFB) and validated our interpretation of BTS predation risk and Sáli population dynamics. Pollock et al. (2019) reported high fledgling mortality from BTS predation (0.41) in 53 days, whereas all other life stages appeared to have much reduced BTS encounter rates. Using our mortality risk for Sáli fledglings in an encounter (0.87), a predation rate of 0.41 over 53 days translated to a nightly encounter rate of 0.012, or 0.52 over 2 months. We defined a model that allowed BTS to encounter fledglings only and simulated 200 random populations with nest success set to 0.50 for natural nests, 0.82 for nest boxes (Savidge et al., 2018), or an intermediate value 0.66.

RESULTS

Avifauna demographics without BTS predation

Stochastic variation in simulated growth rates indicated notable variability in potential growth rates both at the outset of a reintroduction and later as population dynamics equilibrate. Although most simulated populations grew, as would be predicted from $\lambda > 1$, the decline of some simulated populations in the initial years demonstrated the potential for decline due to demographic stochasticity alone, especially in the transient run-up to the stable nonzero equilibrium.

Our simulations indicated that as many as 10 years would be needed for populations to asymptote to a stable population age structure, a phenomenon not uncommon as the realized population growth rate often differed from the eventual asymptotic growth rate at equilibrium (Koons et al., 2006). Within this transient phase following simulated release (Figure 2a), Åga populations were the only one to consistently grow (i.e., $\lambda > 1$), whereas all others showed potential for decline (see overlap of initial 5-year boxplots with $\lambda = 1$ the dashed gray line in Figure 2a). Given the founding population consisted entirely of adults, high adult survival likely explains the initial high growth rate (amplification) for Åga, which quickly settled down near the asymptotic growth rate in the next 5-year period, presumably as founders were

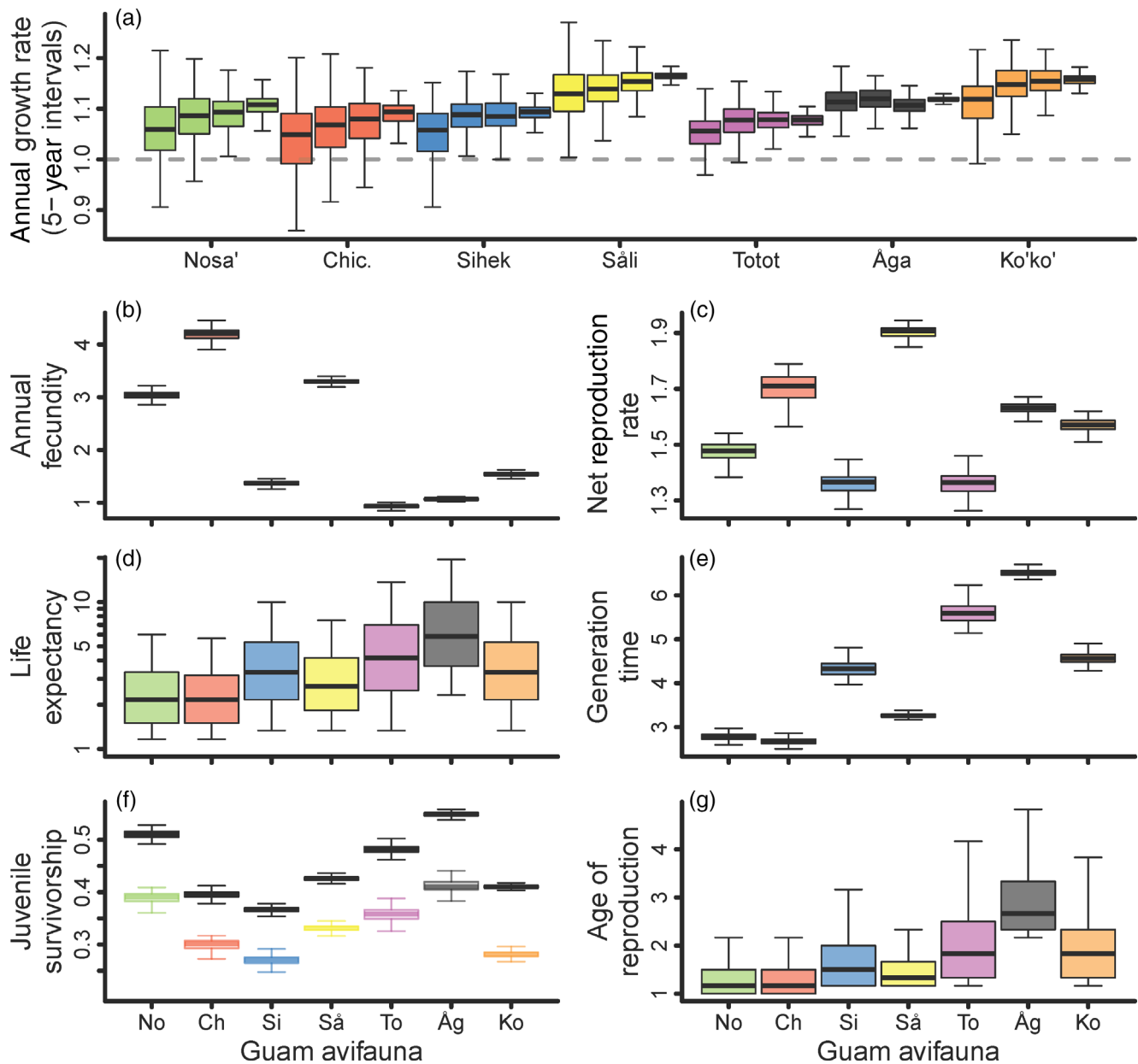


FIGURE 2 Comparison of demographics and life history among Guahan avifauna (No, Nosa'; Ch, Chichirika; Si, Sihek; Sa, Sali; to, Totot; Ag, Aaga; Ko, Ko'ko'). Boxplots display the quantiles and range of output from 200 simulated populations. (a) Annual growth rate was calculated in four consecutive 5-year intervals (e.g., 0–5, 6–10 years). (b) Annual fertility (number of young fledged per year), (c) net reproductive rate, (d) life expectancy (in years), (e) generation time (in years), (f) probability of survival to adulthood (black outline) shown together with probability of survival to first reproduction (color coded outline), and (g) age of first reproduction (in years).

slowly replaced by recruits. Low initial growth rates (attenuation) for simulated releases of all other birds were followed by a steady climb toward an asymptotic rate. Variance in growth rates also stabilized as populations approached equilibrium, with growth rates ranging entirely above one for all birds after 15 years (Figure 2a). Without BTS predation, our simulations for Nosa' and Chichirika indicated a 0.4% and 1.5% risk of extinction within 30 years, compared with no risk of extinction for the other species.

Overall, our models were consistent with the known biology of each of our focal species, capturing the distinct life histories among them. Birds with high juvenile survival rates also had high probabilities of survival to adulthood (Figure 2f). Early maturity boosted Nosa' to a high probability of survival to adulthood, and Aaga had the highest probability of survival to adulthood (Figure 2f), which reflected the fact that Aaga had the highest juvenile survival rate among our focal species (0.638, Faegre et al., 2021). Age of maturity was fixed in our models, but

age of first reproduction was realized stochastically in simulations depending on pair availability and occurred on average a few months after maturity (Figure 2g). This delay was much longer for Ko'ko' and Sihek, almost 1 year on average (Figure 2g), due to their probabilities of pair bonding being <1.0 (Table 1). However, variation in age of reproduction was considerable for all species (Figure 2g), and these delays in reproduction following maturity meant fewer birds survived to reproduce than those surviving to adulthood (lighter versus darker boxes in Figure 2f, respectively).

Life expectancy differences among birds reaching adulthood largely reflected, as it should, adult survival rates (Table 1 and Figure 2d). Åga adults had the greatest life expectancies of our focal species. Generation time, defined as the mean age of reproductive females (Caswell, 2001), varied from <3–7 years among birds (Figure 2e) and followed the same pattern as life expectancy and age of reproduction (Figure 2d,g). Setting an age of senescence in our models effectively inhibited simulated birds from having unreasonably long lifespans. Without senescence, some birds in projections lived for 30–40+ years. To prevent this, we dropped the survival rate to 0.20 for all birds older than the age of senescence (Table 1). With senescence added in this way, maximum lifespan was consistently 5 years beyond the age of senescence listed in Table 1. Average life expectancy was unchanged by our lifespan limit, and population growth only decreased by 1%–2%.

Differences in fledging rates and the propensity to reneest among these birds translated through in our population dynamic metrics to fecundity differences. Nosa', Chichirika, and Sâli all produce small clutches, can reneest rapidly, and achieved the highest annual fecundity rates in our models (Figure 2b). Net reproductive rate, which measures the expected reproductive output of every individual born into a population (Caswell, 2001), exhibited a similar but less pronounced pattern (Figure 2c).

Resilience to BTS predation pressure

Simulating BTS predation in our models showed unequivocally that all our focal birds were highly susceptible to BTS. Populations quickly declined with anything other than extremely low BTS predation risk (Figure 3). Mortality resulting from a BTS encounter can vary by species and life stage (e.g., nestling, adult). We therefore used consensus judgments (McElderry et al., 2021) to estimate a mortality risk in an encounter for each life stage to estimate overall population lambda given BTS encounter rates. Even at our lowest mortality risk on

encounter (light gray line in Figure 3 inset), a very optimistic scenario, simulations indicated that birds of any species could not persist until the chances of being encountered by a BTS were <4% within 2 months (Figure 3). This 2-month rate corresponds to a 0.07% nightly contact rate (Figure 4). Increasing mortality risk per encounter from this optimistic scenario not only reduced population growth rates but also increased the slopes of response curves (cf. light and dark lines in Figure 3). In other words, the higher the risk of mortality on encounter, the more quickly each bird population declined in response to increasing encounter risk (Figure 3). Notably, these response curves at each level of mortality risk appeared consistent among our focal species (Figure 3), with larger birds having a higher chance of survival given an encounter. However, far more important was overall rates of encounter with BTS. The range of encounter rates at which each bird population began to persist, that is, when $\lambda > 1$, indicated the threshold BTS encounter rate for each species over the range of uncertainty in mortality risk on encounter (color-shaded region in Figure 3). Within these uncertainty ranges, our best estimates of mortality given an encounter fell in different parts of the range for different species (colored lines and arrows in Figure 3). Our largest birds (Ko'ko', Åga) and smallest birds (Nosa', Chichirika) were at the optimistic and pessimistic ends, respectively, while medium-sized birds (Sihek, Sâli, Totot) were intermediate.

Sâli on AAFB

In our simulation imitating the persistent Sâli population on Guåhan, we found declining populations for natural nest nests ($\lambda = 0.97$), growing populations with nest boxes ($\lambda = 1.10$), and approximately stable populations with an intermediate nest success ($\lambda = 1.03$). High simulated mortality among juveniles produced a highly skewed age structure (5% fledgling, 14% juvenile, 81% adult) that was similar to that reported in the wild by Pollock et al. (2021): 1% fledgling, 8% juvenile, and 91% adult.

Sensitivity to BTS management

The translation of BTS encounter rates between a 2-month time scale in our models and a nightly rate that is common for BTS monitoring is a strongly nonlinear function (Figure 4). A seemingly mild 1% nightly risk of BTS encounter translates to a high 45% chance of a BTS encounter within 2 months. Given the high risk of

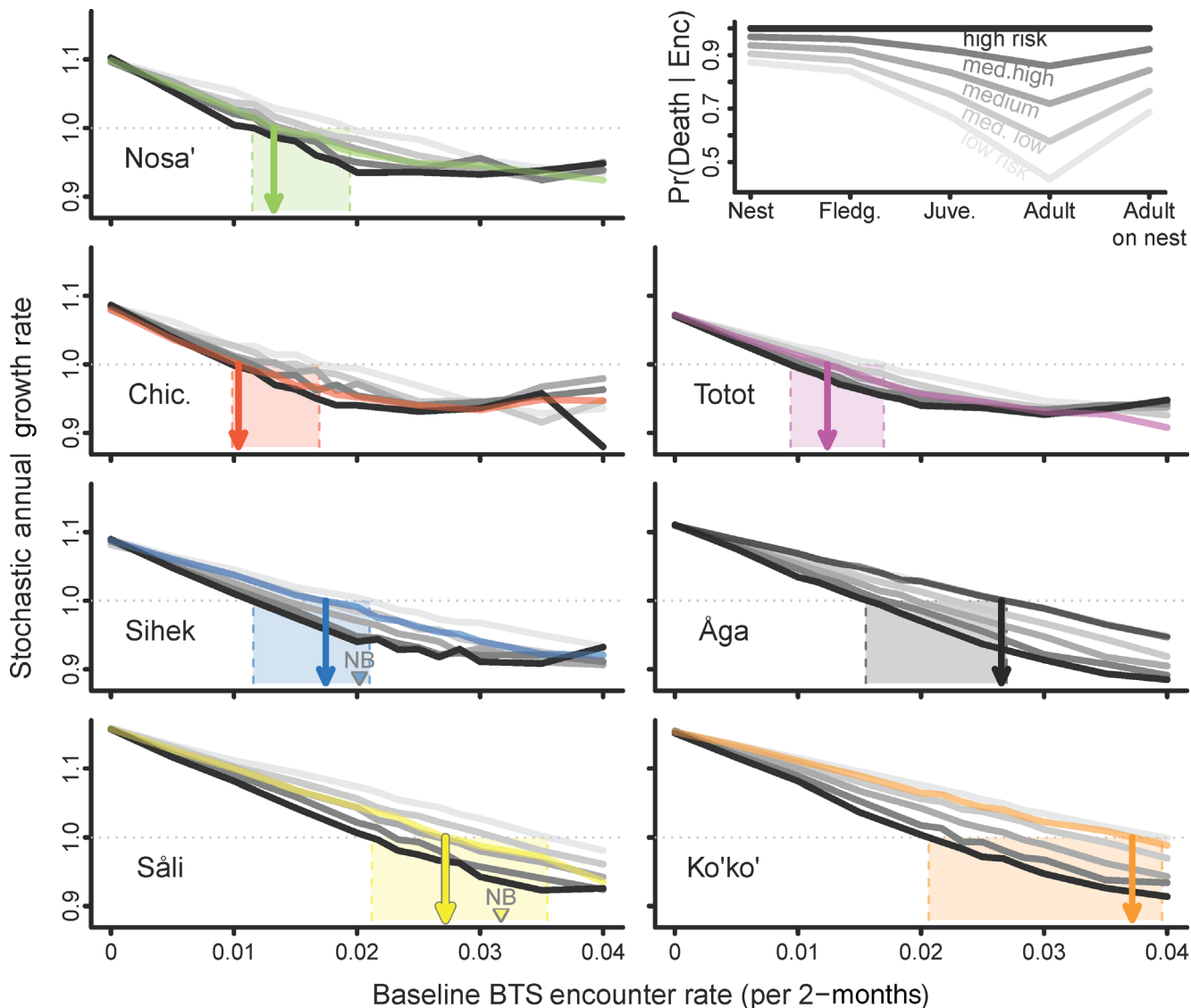


FIGURE 3 Sensitivity of annual rate of stochastic population growth for each bird species to nightly chance of being encountered by a brown treesnake. Solid grayscale lines depict increasing probability of consumption according to inset graph in top right. Colored lines trace the expert-defined mortality risk on encounter. Dashed colored lines delineate the range of encounter rates defined by the range of consumption rates that yield replacement population growth, and the arrow marks the best estimate. Results from simulated nest boxes are marked with a triangle and “NB.”

mortality on encounter and that all stages are at risk, this would mean near 45% mortality per 2 months for the population, which is unsustainable. This scaling of a measurable nightly contact rate up to a risk of encounter that is relevant to a bird helps to translate between management metrics and biological outcomes. Both nightly contact rates and expected bimonthly chance encounters are relevant considerations because we need efficient and easily interpreted monitoring metrics for BTS that also relate to predation risk for birds released in BTS suppressed areas. Our threshold BTS encounter rates translated to nightly contact rates indicate that all birds included in our study have much lower (more than four

orders of magnitude) tolerance to BTS than the currently reported contact rates in managed areas on Guåhan (Figure 4) (Yackel Adams et al., 2019; S.R. Siers, unpublished data).

Among our seven focal species, our models indicated the following ranking in terms of tolerance to BTS: Ko'ko' (highest), Sali, Åga, Sihek, Nosa', Totot, Chichirika (lowest). Our best estimates of threshold BTS nightly contact rates for these birds range from 0.0002 to 0.0006 (Figure 4), or roughly 0.07–0.20 annually. Simulating nest boxes that protected nesting adults and nestlings from BTS encounters had a relatively small effect on threshold BTS contact rates for Sihek and Sali

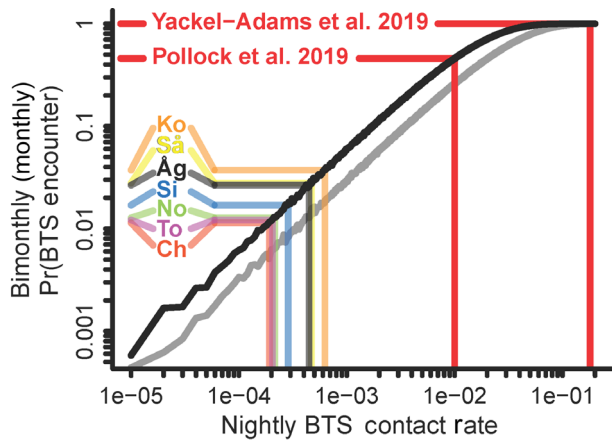


FIGURE 4 Translation of a nightly contact rate to the probability of a bird being encountered by brown treesnake at least once within either a two (black) or one (gray) month period. Dashed lines trace encounter rates between periods. In red is the contact rate measured by Yackel Adams et al. (2019) and Pollock et al. (2019). Species-specific lines correspond to arrows in Figure 3 and trace maximum bimonthly encounter rates under which each bird could persist back to a nightly encounter rate.

(Figures 3 and 5). The choice between simulating BTS encounters at the breeding-pair or individual level appeared to affect the range of uncertainty more than the mean expected threshold (Figure 5). Central to this ranking is the intrinsic rate of population growth (λ).

DISCUSSION

Our simulations of native Guáhan birds' population dynamics under variable predation levels by BTS allowed us to reduce uncertainty in bird reestablishment thresholds to a quantifiable range and to establish a predation-level metric that links forecasts of reintroduction success directly to predator control tactics and monitoring criteria. We accomplished this by (i) piecing together the available demographic information for seven bird species and simulating bird population dynamics, (ii) separating BTS predation into two components: encounter probability and fate on encounter, (iii) quantifying the individual vulnerability of each life stage for each bird species, and (iv) simulating BTS encounters and bird fate following an encounter in virtual founding populations. Because we cannot directly observe snake–bird interactions on Guáhan, because the snakes have largely extirpated Guáhan's birds, we utilized expert judgment to parameterize the outcomes of bird–snake interactions (described in McElderry et al., 2021). Further, we bypassed uncertainty in snake density by focusing on the rate at which birds might be encountered by BTS, which is a metric

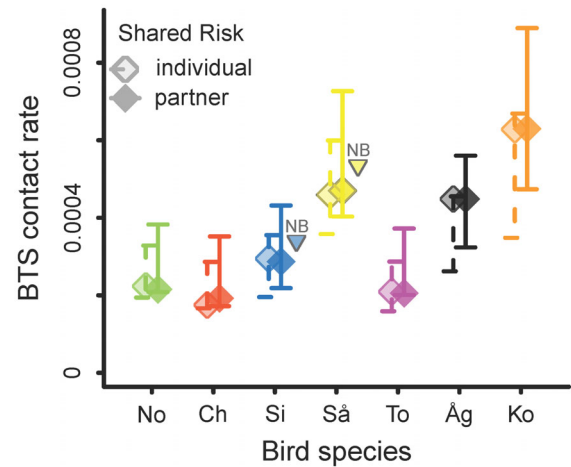


FIGURE 5 Threshold (minimum) brown treesnake contact rate at which each bird species might persist. Diamonds indicate the results using expert estimates for mortality risk on encounter (McElderry et al., 2021), and confidence intervals represent the range of mortality bracketed in Figure 3. Dotted lines with open diamonds represent individual level encounters, and solid lines and diamonds represent family-level encounters. Results from simulated nest boxes are marked with a triangle and “NB.”

that can be measured in the field and serves as a direct link between birds and snakes in our model. We believe our predation threshold metric provides an important management tool to help identify target BTS suppression levels that can help increase the likelihood of success for future bird reintroduction campaigns.

Threat assessment

The rapid decline and loss of Guáhan's birds clearly showed they could not persist with an uncontrolled population of BTS in Guáhan's forests (Savidge, 1987; Wiles et al., 2003). Our models indicated that current predation levels would have to be reduced substantially to allow for bird persistence. The thresholds we identified here appear far beyond current suppression capabilities at a landscape level, but focused efforts in smaller areas may be feasible. Ramping up suppression efforts in confined areas may lessen this gap locally, but new tactics, such as targeting juvenile BTS before they mature and reproduce, may be required to approach this extremely low estimated predation threshold. If this threshold cannot be reached, our results indicate that bird reintroductions will fail. Despite seemingly large differences among birds in vulnerability to BTS (McElderry et al., 2021), the range of tolerable predation rates is rather narrow relative to the amount of reduction in current BTS levels required.

Thus, any discussion of which bird might be our best candidate for reestablishment is secondary to discussing how these reduced predation thresholds might be reached at a scale that could support viable bird populations.

BTS range in size from 350 mm SVL hatchlings to >2000 mm for very large males (Savidge, 1991; Siers et al., 2017a), and the size distribution of a population is an important determinant of the rate of lethal encounters suffered at each bird life stage (McElderry et al., 2021). Reliable BTS density estimates over Guåhan's landscape have proven to be elusive, and well-defined size distributions require intensive sampling (Amburgey et al., 2021; Rodda et al., 2007; Siers et al., 2017b, 2021; Siers, Shiels, & Barnhart, 2020), but new techniques that extract size frequency data from camera traps (Siers, 2021) may provide this key information for snakes that respond to live lures. Snake size is innately linked to prey selection (Lardner et al., 2009; Savidge, 1987; Siers, 2015) and is strongly believed to affect predation threat for endothermic prey of varying size (McElderry et al., 2021; Siers et al., 2017a), but we did not explicitly simulate various snake sizes. Instead, our simulated range of mortality risk per encounter can be viewed as a surrogate for a range of snake sizes if we consider that an area's contact rate is a reflection of foraging differences among snake sizes. Our model summaries were based on our elicitation (McElderry et al., 2021), and therefore assumed medium-sized mature snakes on average, but if we were to suspect on average larger snakes in an area, we could simply shift the threshold to a higher mortality risk for each encounter. BTS control efforts tend to be more effective for certain size classes (Lardner et al., 2013), and an actively controlled BTS population may develop an altered size distribution, depending on the suppression method (Nafus et al., 2020, 2022). In those cases, models that more explicitly track snake size distributions in a particular area of interest could be developed to increase forecast accuracy as actual size distributions of snakes encountering lures are documented (e.g., Siers, 2021).

We modeled the inherent growth rates of bird populations with threats limited to BTS predation to focus on identifying snake predation thresholds, but if there are other important sources of mortality in a species, then the true range of maximum predation thresholds may be lower than we estimated. Although the estimates of survival and productivity from the literature that we used incorporated background effects of other predation sources, specific inclusion of other threats in our model would result in even lower BTS predation levels necessary to reach a stable or growing population trajectory. Even in the absence of predation, variability among simulated populations for all focal birds indicated the possibility for population decline during the initial

postrelease period due to demographic stochasticity. We did not model environmental stochasticity, but a sequence of several unfavorable years could reduce the chances for success of reintroduced populations. For Nosa' and Chichirika, random stochastic processes can cause a high risk of decline for 10 or more years. Even in the absence of introduced predators, such risks are not uncommon, as indicated by surveys of past reintroductions that show that success is positively associated with the number of individuals released (Fischer & Lindenmayer, 2000; Griffith et al., 1989; Wolf et al., 1996), but the number of individuals released may also be related to the initial perception of success (Armstrong & Seddon, 2008).

Even with suppressed BTS levels, many of the species we modeled may present difficult reintroductions for other reasons. For example, field surveys for Nosa' and Chichirika (Naabak) on other islands in the CNMI indicate variable population growth over time, with a long-term trend of general decline or no trend (Camp et al., 2015; Ha et al., 2018; Saracco et al., 2021). Similarly, Totot and Sihek in captivity show only moderate population growth $\lambda = 1.047$ and 1.004 , respectively (Melton et al., 2016; Newland et al., 2020). Åga appears to be threatened by disease (Faegre et al., 2019), whereas Sihek is threatened by inbreeding depression (Trask et al., 2021). Additionally, all of these birds are threatened by other nonnative predators such as monitor lizards, cats, rats, and dogs (Beauprez & Brock, 1999b; Faegre et al., 2019; Pollock et al., 2019), and some of these birds may compete with each other if confined in small BTS exclosures (Fontenot et al., 2006; Nietmann & Ha, 2018). Although we focused our modeling scenarios on varying levels of BTS predation, these other factors may also be important to consider and mitigate for successful reintroductions back to Guåhan. Thus, our results only address the additional pressures from BTS predation, assuming moderate background levels of mortality. However, other threats pressuring populations would need to be evaluated and simultaneously mitigated along with BTS suppression efforts.

Mitigation strategies

Although model results indicate that BTS levels would need to be greatly reduced at the landscape level to allow the persistence of forest birds, species may be able to persist in smaller areas where BTS are severely suppressed or if certain stages of a bird's life cycle are protected. An example is Sáli on AAFB, where the combination of lower BTS levels in the developed areas of the base and safer nest sites (typically anthropogenic structures) and

snake-proof nesting boxes (Savidge et al., 2018) appear to have allowed this species to persist on the base and several other urban areas (Pollock et al., 2021). Our simulation of Sáli on AAFB produced population metrics congruent with reported metrics. Similarly to Pollock et al. (2021), we showed that high juvenile mortality produced a skewed age structure composed mostly of adults. We also found evidence to support the claim that nonnatural nest sites, including nest boxes, may be crucial for Sáli's persistence on AAFB. Thus, conservation strategies that reduce BTS predation at specific parts of a species' life cycle, or in finite areas, may be successful even when larger landscape-scale suppression is not possible.

An alternative scenario is the 55-ha Habitat Management Unit (HMU) on AAFB in northern Guåhan, which has been proposed as a site for trial reintroductions. The HMU is enclosed by a predator-exclusion fence, and low BTS levels are being achieved there by aerial application of toxic baits inside the fence (Siers, Eisemann, et al., 2020; Siers, Savidge, & Demeulenaere, 2017). Coupled with a core BTS exclusion area, aerial delivery of BTS toxicant in the forest areas outside the HMU could reduce BTS levels in the surrounding area where mobile birds are likely to wander. Such a mix of targeted local and regional general BTS suppression centered on a BTS enclosure may hold the most promise at reaching the very low threshold of predation levels, within the enclosure, that our models indicate are necessary for reestablishment.

If BTS can be suppressed to contact rates below our maximum threshold, and if other threats are also sufficiently mitigated, our models indicate that Sáli and Ko'ko' would be the best candidates for trial reintroductions. Sáli in particular may be the best candidate for release in an enclosure, for two main reasons: It is already on Guåhan in relatively high abundance but limited in distribution (Pollock et al., 2021), and its behavior, specifically the use of snake-proof nest boxes and safer roost sites, reduces the pressure of predation from key parts of their life cycle (Pollock et al., 2019; Savidge et al., 2018; results herein). Trial releases with a bird that already occurs on Guåhan and is not endangered would allow ground truthing of our model predictions while providing room for error and adjustment before attempting to release more sensitive bird species with smaller global population sizes. By monitoring a founding population of Sáli in a BTS suppressed forest, bird demographic rates could be more directly linked to snake contact rates (e.g., Armstrong et al., 2006). Predictions could then be updated and the thresholds for reintroducing the next promising candidate (which our results indicate could be Ko'ko') could be refined.

Previous experimental releases of Ko'ko' in a 24-ha forest plot with BTS density reduced by trapping (Area 50 on AAFB) demonstrated that the species could breed successfully under conditions of reduced BTS predation (Beauprez & Brock, 1999b), but snake suppression was not maintained long enough to evaluate the long-term persistence of Ko'ko' under such conditions (D. Vice, Guam Division of Aquatic and Wildlife Resources, written communication, 2020). Failure of this attempted reintroduction on Guåhan may have been due to cat predation (Beauprez & Brock, 1999b), which was the primary source of mortality in a simultaneous Ko'ko' release on Luta (Beauprez & Brock, 1999a). Cat removal is likely as important as BTS suppression for Ko'ko' and may be crucial for all of these birds. Cat predation has also been reported as a source of mortality for Åga on Luta (Faegre et al., 2016; Zarones et al., 2015), but current data indicate this may be less of a factor (Faegre et al., 2021). Åga would be the third candidate for reintroduction, but reports of low fecundity (Zarones et al., 2015) may indicate additional hurdles to reintroduction beyond reduced BTS levels.

The two smallest birds, Chichirika and Nosa', along with the larger Totot and the Sihek, appear to be relatively sensitive to areas with any measurable BTS predation risk. If Sihek could be shown to reliably use artificial nest boxes with a founding population that had a high intrinsic rate of increase, then Sihek might be able to persist in areas where there were suppressed BTS levels. However, even with protection of nesting areas, if Sihek roost in areas where they can be encountered by BTS, then the daily risk would still have to be very low in order for the population to persist. Because Sihek is the rarest of our seven birds and remains extinct in the wild, attempts to reintroduce other species with greater global numbers first would be important to build confidence in methods and predictions. The intention to perform conservation introductions of Sihek to small, isolated islands in the Pacific has been expressed (Trask et al., 2020, 2021), and if those efforts are successful and produce excess young, then those young could be the source for future reintroductions into Guåhan when conditions are suitable. Additionally, monitoring studies from these introduced populations would provide valuable demographic information to optimize our models and increase the accuracy of our predictive models.

Achievement benchmarks

In the period just after peak bird loss, BTS were suspected to occur at densities near 100 per hectare on Guåhan (Rodda et al., 1992). More recently, densities were

believed to be near 25 snakes per hectare, although density varies across the landscape (Christy et al., 2010; Rodda et al., 1999; Tyrrell et al., 2009). In terms of contact rates, Yackel Adams et al. (2019) reported 0.18 contacts per lure per night, but repeat visits from the same snakes are difficult to discern. From Pollock et al. (2019), we estimated a nightly contact rate between fledglings and BTS of 0.012 on AAFB. Both of these BTS contact rates would result in predation rates well above the minimum threshold levels we predict necessary for bird population persistence (Figure 5).

One of the key challenges to using our models to help guide future reintroductions is linking modeled encounter rates in the model with true encounter rates that birds would experience in the wild. Live animal lures in cages can be used as a surrogate for a nest or roosting bird, and how long the lure can persist on the landscape before being encountered by a snake large enough to be lethal can be measured, providing a contact rate for measuring potential predation rates and setting control targets. As a method of indexing BTS predation threat in snake-suppressed areas, one of the authors (SRS) is developing a standardized system for using cameras to estimate contact rates between free-ranging BTS and live lures (mice or birds in protective chambers; e.g., Siers, 2021; Yackel Adams et al., 2019). Such contact rates may be the only practical index for estimating BTS attack rates on birds in each area under consideration. We project that an estimated predation rate below 0.0006 contacts per lure per night is approximate to the upper predation threshold, below which these seven birds might persist. Upon approaching this threshold, a crucial next step would be to verify in the field these predictions and fine-tune benchmark suppression goals with improved accuracy and preferably with a better representation of BTS abundance dynamics.

Our work addresses the increasingly common scenario around the world of introduced predators that threaten native species but cannot be completely excluded or eradicated from areas of conservation concern. In our case, the stark impacts of BTS cannot be overstated; the species has caused the extinction of most of Guåhan's birds in just a few decades. Removing this predator or suppressing its densities to levels indicated from our work would be a key component in restoring Guåhan's avifauna. Although the effects of BTS on Guåhan avifauna are well documented, it remains a key case study exemplifying the broad possible impacts of a single invasive species, and our work demonstrates just how far suppression efforts would need to go to overcome these impacts.

AUTHOR CONTRIBUTIONS

Initially conceived by Shane R. Siers and Eben H. Paxton, this project was designed with input from all authors and

executed by Robert M. McElderry with guidance from Shane R. Siers and Eben H. Paxton. Andre V. Nguyen gathered demographic information. Robert M. McElderry designed the models, wrote the computer code, and composed the initial manuscript draft and the appendices. Shane R. Siers secured funding.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (McElderry et al., 2022) are available from Figshare at <https://doi.org/10.6084/m9.figshare.19251713.v2>.

ORCID

Robert M. McElderry  <https://orcid.org/0000-0002-3906-1447>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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