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Pervasive impacts of invasive brown treesnakes drive low fledgling survival in endangered Micronesian Starlings (*Aplonis opaca*) on Guam

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ABSTRACT

Invasive predators have caused widespread loss of biodiversity in island ecosystems, yet certain species are able to tolerate the presence of generalist invaders. For example, the invasive brown treesnake (BTS; *Boiga irregularis*) caused the extirpation of 10 of 12 native forest bird species on the island of Guam, but a remnant population of the Micronesian Starling (*Aplonis opaca*), or Såli, has managed to persist on a military installation in northern Guam. Understanding how Micronesian Starlings are coping with the presence of BTS can inform conservation efforts for island bird populations facing invasive predators and provide insight into strategies for expanding the starling population. We monitored the survival, movements, and habitat use of 43 radio-tagged starling fledglings during this vulnerable life-history stage. Invasive predators accounted for 75% of fledgling mortality (56% from BTS; 19% from feral cats) and contributed to one of the lowest post-fledging survival rates (38% through day 21 post-fledging) recorded for passerine birds. Predation by BTS persisted at elevated rates following natal dispersal, further reducing cumulative survival to 26% through 53 days post-fledging. Nest location was an important predictor of survival: fledglings from nest boxes closer to the forest edge were more likely to use forest habitat at younger ages and more likely to be depredated by BTS. Overall, our findings indicate that BTS continue to severely impact Guam's starling population, even more so than invasive predators affect native birds in other island systems. We recommend deploying nest boxes farther from the forest to improve fledgling survival and implementing urban predator control to promote growth of the Micronesian Starling population on Guam and facilitate future reintroductions of other species.

Keywords: brown treesnake, fledgling survival, Guam, invasive species, islands

Los impactos múltiples de la serpiente invasora arborícola *Boiga irregularis* generan la baja supervivencia de los volantones de la especie en peligro *Aplonis opaca* en Guam

RESUMEN

Los depredadores invasores han causado una amplia pérdida de biodiversidad en los ecosistemas isleños, aunque algunas especies son capaces de tolerar la presencia de invasores generalistas. Por ejemplo, la serpiente invasora arborícola *Boiga irregularis* causó la desaparición de 10 de 12 especies de aves nativas de ambientes boscosos en la isla de Guam, pero una población remanente de *Aplonis opaca* se las ha arreglado para sobrevivir en un complejo militar en el norte de Guam. Entender cómo *A. opaca* se las está arreglando con la presencia de *B. irregularis* puede permitir mejorar los esfuerzos de conservación de las poblaciones de aves de la isla que están lidiando con los depredadores invasores y puede brindar información sobre las estrategias para expandir la población de *A. opaca*. Para ello, seguimos la supervivencia, los movimientos y el uso de hábitat de 43 volantones de *A. opaca* marcados con transmisores durante este período de vulnerabilidad en la historia de vida. Los depredadores invasores representaron el 75% de la mortalidad de los volantones (56% por *B. irregularis*; 19% por gatos asilvestrados) y contribuyeron con una de las tasas más bajas de supervivencia post-emplumamiento (38% hasta el día 21 post-emplumamiento) registradas para las aves paserinas. La depredación por parte de *B. irregularis* persistió a tasas elevadas luego de la dispersión natal, reduciendo más aún la supervivencia acumulada al 26% hasta los 53 días post-emplumamiento. La localización del nido fue un predictor importante de la supervivencia: los volantones provenientes de cajas nido más cercanas al borde del bosque presentaron mayor probabilidad de usar el hábitat boscoso a edades más tempranas y mayor probabilidad de ser depredados por *B. irregularis*. De modo general, nuestros resultados indican que *B. irregularis* continúa impactando severamente la población de *A. opaca* de Guam, incluso más de lo que los depredadores invasores afectan a las aves nativas en otros sistemas de islas. Recomendamos colocar cajas nido a mayores distancias del bosque para mejorar la supervivencia de los volantones e implementar el control de los depredadores urbanos para mejorar el crecimiento de la población de *A. opaca* en Guam y facilitar futuras reintroducciones de otras especies.

Palabras clave: *Boiga irregularis*, especies invasoras, Guam, islas, supervivencia del volantón

INTRODUCTION

Invasive species can have profound negative impacts on ecosystems, including loss of biodiversity (Lowe et al. 2000, Blackburn et al. 2004, Clavero et al. 2009), altered community structure (Sanders et al. 2003), and disruption of ecosystem functioning (Crowl et al. 2008, Rogers et al. 2017). Island ecosystems are particularly susceptible because they often have high levels of endemism (Kier et al. 2009) and harbor native species that have evolved in geographic isolation with no shared evolutionary history with invasive species (Blackburn et al. 2004, Medina et al. 2011). Consequently, human introductions of alien species—particularly predators—to island ecosystems with few competitors and abundant resources have had devastating effects on local biodiversity (Fritts and Rodda 1998, Hutton et al. 2007, Bell et al. 2016).

An iconic example of this phenomenon is the introduction of the brown treesnake (BTS; *Boiga irregularis*) on Guam, an island with no native predators of birds. BTS are nocturnal, arboreal colubrid snakes that are generalist predators of both small (i.e. frogs and lizards) and large (i.e. birds and mammals) vertebrates (Savidge 1988, Greene 1989). Following their accidental introduction from Australasia after World War II (Rodda et al. 1992), BTS established a population and quickly spread throughout the island, depredating ecologically naïve birds and devastating the avifauna (Savidge 1987, Fritts and Rodda 1998). Within decades, BTS caused the complete extirpation of 10 of 12 (83%) native forest bird species (Savidge 1987).

While the broad impacts of BTS on Guam's native birds are well documented (Savidge 1987, Wiles et al. 1995, Wiles et al. 2003), most population declines occurred rapidly and synchronously (Wiles et al. 2003), precluding a mechanistic understanding of how BTS drove the avifaunal collapse. As a result, previous studies were unable to quantify the impacts of BTS during specific life-history stages of affected species, including the sensitive and understudied post-fledging period (i.e. the time after a bird leaves its nest but before it migrates or disperses from the natal territory; Cox et al. 2014). Young birds are often most vulnerable immediately after fledging (Sullivan 1989, Weathers and Sullivan 1989) and avian population growth rates can be strongly influenced by first-year survival and recruitment of new individuals into the population (Cox et al. 2014). Previous studies have identified several factors that influence post-fledging survival rates, including intrinsic sources of variation such as fledgling body condition (Naef-Daenzer et al. 2001, Vitz and Rodewald 2011, Maness and Anderson 2013) and wing development (Jones et al. 2017b, Martin et al. 2018) and extrinsic sources such as habitat use (Vitz and Rodewald 2011, Cox et al. 2014, Jones et al. 2017a) and predator type or abundance (Balogh et al. 2011, Haché et al. 2014). Characterization of post-fledging survival

rates is an essential component of determining the factors that influence avian population growth and stability (Cox et al. 2014). Obtaining a more mechanistic understanding of the demographic impacts of BTS may help inform management strategies for restoring bird populations on Guam and potentially on other island systems facing nocturnal invasive predators.

To understand how BTS are currently affecting native bird populations on Guam, we conducted a case study on the Micronesian Starling or Såli (*Aplonis opaca*), 1 of only 2 native forest bird species persisting on the island (Wiles et al. 2003). We used radio-telemetry to investigate the post-fledging survival of starlings relative to their patterns of movement and use of habitat, providing a unique opportunity to measure demographic impacts of BTS during a highly vulnerable life-history stage. Our goals were threefold: (1) to quantify the rates of mortality of starling fledglings caused by BTS and other sources to understand their relative demographic impacts; (2) to determine the influence of intrinsic (i.e. body mass, body condition, body size) and extrinsic (i.e. nest location, brood size, predator type) factors on variation in fledgling survival; and (3) to use fledgling survival data to inform management of the starling population on Guam and provide insight into the threats that nocturnal invasive predators may pose to other island bird populations.

METHODS

Study Site and Species
We conducted our study of Micronesian Starling fledglings from April to December 2017 on the island of Guam, the largest (542 km^2) and southernmost island in the Mariana Islands chain in the western North Pacific Ocean. Guam experiences a tropical climate characterized by a distinct dry season (January–June) and wet season (July–December) but little annual temperature fluctuation (mean annual temperature ± SD = 27.45 ± 0.52°C; National Weather Service, https://w2.weather.gov/climate/).

The Micronesian Starling is a medium-sized (71–93 g) omnivorous passerine distributed throughout Micronesia (Craig and Feare 2017). On Guam, it is restricted primarily to Andersen Air Force Base (13.57°N, 144.92°E), an 8100-ha military installation on the northern part of the island (Figure 1). Our study site on the base encompassed a mosaic of habitats, including urban housing areas, a golf course, degraded mixed forest, and primary limestone forest. While the population in northern Guam was estimated at only 50–100 individuals in the early 1990s (Wiles et al. 1995), the current level appears to be several times that number (H. S. Pollock and M. Kastner personal observation). Persistence may have been facilitated by the species' tolerance to urbanization. Starlings currently nest and roost in urban and suburban areas on Guam (H. S. Pollock

and M. Kastner personal observation), which contain habitat features that deter snakes, such as high nocturnal illumination and large roads (Campbell et al. 2008, Siers et al. 2014). Furthermore, active efforts to trap and remove BTS from Andersen Air Force Base, where BTS suppression has occurred since 1993, have reduced BTS abundance (Vice and Pitzler 2002). Control methods include trapping BTS using modified minnow traps baited with live mice (Vice et al. 2005) and bait tubes containing dead mice implanted with acetaminophen (Savarie et al. 2001). There is a stark forest–urban ecotone around the perimeter of Andersen Air Force Base (Figure 1), and these control methods impede BTS encroachment into residential areas.

Bird Capture, Handling, and Radio-telemetry

To trap and radio-tag fledglings, we took advantage of nest boxes that were deployed as part of a recently implemented conservation effort to increase the starling population (J. A. Savidge personal observation). Nest boxes were situated on concrete utility poles (n = 50) or electric metallic tube (EMT) poles (n = 25) located throughout the urban housing area 70.4–871.1 m from the discrete forest edge (Supplemental Material Figure S1). We monitored nest boxes every 3–4 days to determine when to band and radio-tag nestlings. We handled nestlings at 2 discrete time points during the nesting cycle. First, we removed nestlings from the nest box at 15 days post-hatching and

banded each with a U.S. Geological Survey metal band and a unique combination of 3 Darvic color bands (Avinet, Portland, Maine, USA) to facilitate individual identification. Second, at 22–23 days post-hatching (2–3 days prior to fledging), we randomly selected 1 nestling per brood and attached a radio transmitter (1.8 g LB-2, Holohil Systems, Carp, Ontario, Canada) using the leg-loop harness method (Rappole and Tipton 1991). Transmitters had a pulse rate of 0.33 pulses per second (i.e. one pulse every 3 seconds) and a battery life of ~175 days. To reduce potential deleterious effects of transmitters on fledgling behavior (Barron et al. 2010), we ensured that the combined mass of the harness and transmitter weighed <4% (3.25 ± 0.34%) of fledgling body mass. We also measured the length of each fledgling's tibiotarsus (hereafter tarsus) using digital calipers (model IP54, EAGems, Palmdale, California, USA; accuracy ±0.01 mm) and its body mass using a digital scale (AWS-201, American Weigh Scales, Cumming, Georgia, USA; accuracy ±0.01 g).

To monitor survival, we tracked radiotagged fledglings using hand-held telemetry receivers (model R-1000, Communications Specialists, Orange, California, USA) attached to 3-element Yagi antennas (Wildlife Materials, Murphysboro, Illinois, USA). Because the period of greatest vulnerability is often immediately after fledging, we monitored survival daily from days 0 to 15 post-fledging, 3 times per week from days 15 to 30 post-fledging, and 1–2 times
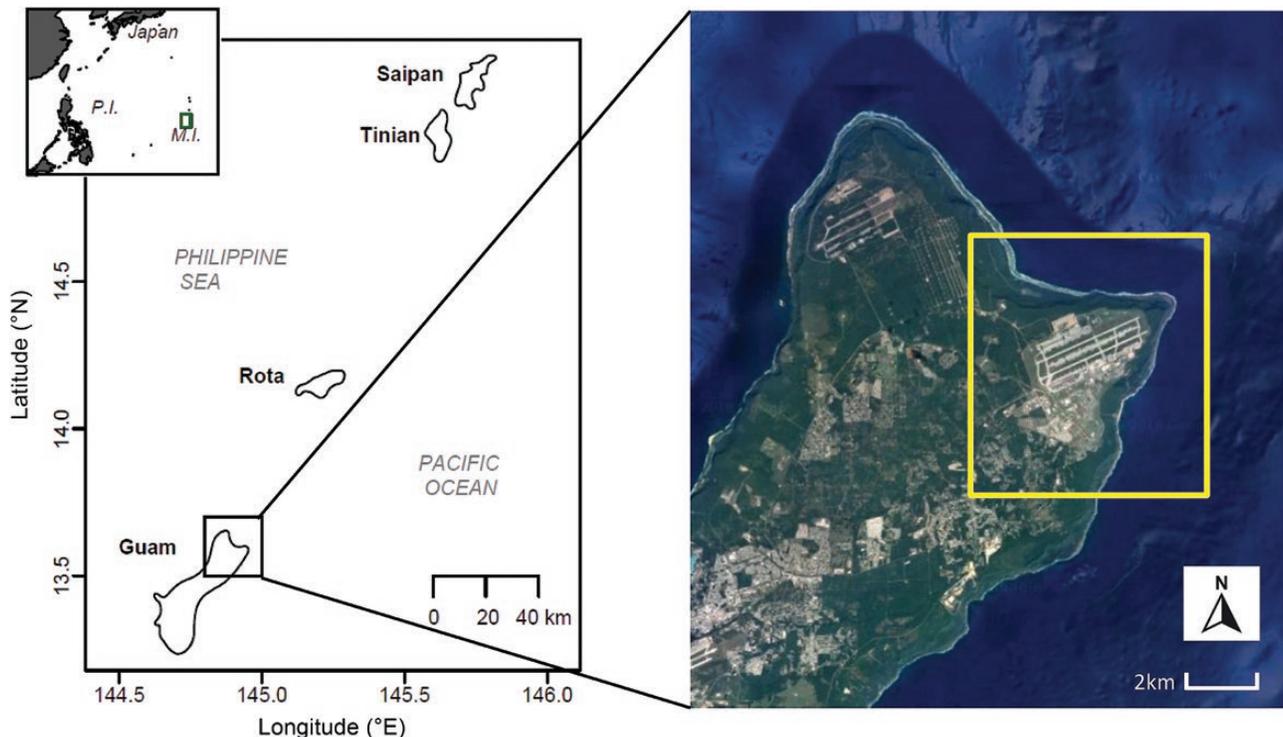

FIGURE 1. (Left) Map of the southernmost islands of the Mariana archipelago. Inset is a map of the western North Pacific Ocean, with the Mariana Islands delineated by the green rectangle. (Right) Satellite imagery of the study area (indicated by the yellow rectangle).

per week after 30 days post-fledging. We obtained visual resights of radio-tagged fledglings, and we recorded perch height, substrate, parental behavior (number of parents present, parental provisioning, and parental alarm calls), and georeferenced locations. We also obtained nocturnal roost locations on a weekly basis for as many of our fledglings as possible because birds are susceptible to nocturnal predation by BTS. When we encountered a dead radio-tagged fledgling, we noted stage of decomposition and any salient information indicating the cause of mortality. We assigned the cause of mortality as follows: (1) BTS predation if the dead fledgling was found inside of a snake, the fledgling had characteristic saliva-matted feathers on the back of its head and shoulders (following Savidge 1988), or its remains were found covered in BTS fecal material; (2) cat predation if the fledgling was partially or completely consumed with legs and wings left behind (H. S. Pollock personal observation; Supplemental Material Figure S1); or (3) exposure if the fledgling was found intact without any signs of predation in combination with recent inclement weather. There are no major avian or mammalian predators on Guam, and therefore we were able to determine the cause of mortality for all but 3 fledglings: 1 killed by an unknown predator and 2 that disappeared from the study area. We assumed that these 2 fledglings died, as they both disappeared at early ages (4 and 8 days), when fledglings have limited mobility and are highly sedentary.

Statistical Analysis
Estimating cause-specific rates of fledgling mortality
. We estimated probabilities of fledgling mortality using a Bayesian framework and multi-state models in program MARK (White and Burnham 1999). Unlike traditional models estimating survival in MARK, multi-state models can incorporate discrete states for each occasion of a capture or resighting while also accounting for transition probabilities among states and uncertainty in state membership when an individual is not observed. Using this feature and following methods in Jones et al. (2017b), we assigned each observation of a fledgling to 1 of 5 discrete states: alive, mortality by BTS, mortality by cat, mortality by exposure, and mortality by an unknown source. For all models, we fixed our survival parameter(s) at 1, fixed the transition probabilities from a dead state to an alive state and from a dead state to a dead state at zero (absorbing states), and estimated cause-specific rates of mortality using transition probabilities from alive to dead states.

Past research has identified age as the main predictor of post-fledging mortality in birds (Sullivan 1989, Weathers and Sullivan 1989, Cox et al. 2014). Thus, before examining the influence of other factors on fledgling mortality, we first refined our models by incorporating an age structure based on past post-fledging studies (Maness and Anderson 2013, Cox et al. 2014, Naef-Daenzer and Grüebler 2016)

and the timing (ages) of fledgling death observed in our study. Our structure included 7 age classes (ages 0, 1, 2, 3, 4, 5–8, and 9+ days post-fledging), which we subsequently used in all models. We then ran additional models in accordance with our a priori hypotheses, in which we incorporated covariate effects of fledgling body mass, body size (tarsus length), body condition (i.e. the residual from a linear regression of tarsus length and body mass; Vitz and Rodewald 2011), brood size, fledging date, and distance (m) of the fledgling's nest box from the forest edge (one covariate per model for a total of 6 covariate models).

We used the Markov chain Monte Carlo (MCMC) option in MARK to estimate the posterior distribution for each of our models. For each model, we fit 10 chains of 50,000 samples with an initial 20,000 iteration burn-in period. We used vague priors (default values in MARK) for all models and checked for model convergence using trace plots and Gelman-Rubin convergence statistics ($\hat{r} < 1.2$). For covariate effects, we based inferences on posterior means and whether 95% Bayesian Credible Intervals (BCIs) overlapped zero (Mordecai et al. 2011). We also estimated cumulative probabilities of survival by multiplying daily survival estimates within 3 time periods: (1) days 0–5 (ages when mortality rates were highest), (2) days 0–21 (the standardized period used to calculate post-fledging survival in Cox et al. 2014), and (3) days 0–53 (past which no fledgling died during our study).

Some fledglings that we radio-tagged (17 of 43) came from nest boxes in which we had previously tagged a fledgling from an earlier brood. Although we never tagged multiple fledglings from the same clutch, the fates of fledglings from the same nest box may not be independent given that they may have the same parents and may experience more similar environmental pressures upon fledging relative to birds from different boxes. Including nest box identity as a random effect could control for this potential nonindependence, but random effects are difficult to incorporate into multi-state models in program MARK (Jones et al. 2017b). To control for nonindependence in fates among box mates, we randomly selected 1 fledgling per box to derive a subset of fledglings from 26 unique nest boxes. We repeated all analyses for this reduced dataset and compared results with the original dataset of 43 fledglings and found qualitatively similar results with respect to covariate effects and overall cause-specific mortality rates (Supplemental Material Tables S1, S2). Because the reduced dataset yielded similar conclusions as the original dataset, we present results from the full dataset (n = 43 fledglings).

Characterizing post-fledging movements and habitat use
. To examine patterns of post-fledging movements and habitat use, we first calculated for each radio-tagged individual the length of the post-fledging period (i.e. the period between fledging from the nest and dispersing from

the natal territory; Cox et al. 2014). We considered birds to have dispersed when they were independent from their parents, which we deemed to have occurred when all of the following criteria were satisfied: (1) fledglings had ceased to exhibit begging behavior, (2) fledglings had joined juvenile flocks and begun foraging independently (Jenkins 1983), and (3) parents had begun nest-building again (Tarwater and Brawn 2010). We used the Point Distance function in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, California, USA) to calculate the distance of each fledgling from its natal nest box throughout the post-fledging period (Yackel-Adams et al. 2001). We summarized mean distances moved by fledglings within 11 different age classes: 0, 1, 2, 3, 4, 5–8, 9–10, 11–15, 16–20, 21–25, and 26–30 days.

To assess use of habitat during the post-fledging period and the weeks following natal dispersal, we used ArcGIS to overlay resighting locations on high-resolution satellite imagery of the study area (National Geospatial Center of Excellence, Fort Worth Federal Center, Fort Worth, Texas; 0.3-m², 8-band multispectral; November 2016). Because BTS are nocturnal, arboreal, and thought to prefer forest habitats (Rodda et al. 1999), we predicted that the proximity of a nest box to forested habitat would be a predation risk for starling fledglings, particularly if they roosted near the natal site. Because there is a stark urban–forest ecotone around the perimeter of Andersen Air Force Base (Figure 1), we used a binary habitat classification (forest vs. urban) to assess both diurnal and nocturnal use of habitat by fledglings. We classified a resighting location as "forest" if it occurred in closed-canopy forest and "urban" if it occurred outside of closed-canopy forest. All values reported below are means ± SE unless otherwise stated.

RESULTS

Sources of Fledgling Mortality

We tagged and monitored survival of 43 starling fledglings, of which 11 (25.6%) survived and 32 (74.4%) died. Of the mortalities, 21 (65.6%) died within 5 days post-fledging, 4 (12.5%) died between days 5 and 8 post-fledging, and 7 (21.9%) died 9 or more days post-fledging. Overall, daily mortality rates were highest during the first 5 days post-fledging, with the daily probability of mortality decreasing to ~1% around day 9 (Figure 2). Cumulative survival for fledglings was 50% through day 5 post-fledging, 38% through day 20, and 26% through day 53. BTS predation was the most common source of fledgling death (56%), followed by cat predation (19%), exposure (13%), and other sources of mortality (13%). Consequently, daily probability of mortality due to BTS was 2–7 times higher than other sources of mortality throughout the post-fledging period (Figure 3). Mortality rates due to BTS predation remained comparatively high even during later stages of the post-fledging period and after natal dispersal (Figure 3), and BTS accounted for 6 of 7 mortality events associated with older fledglings (9+ days post-fledging). We found no effect of fledgling mass, body condition (residuals of tarsus by mass regression), size (tarsus length), brood size, or fledging date on cause-specific rates of mortality (Table 1). However, we did detect an effect of nest location on probability of mortality due to BTS. Birds that fledged from nest boxes located closer to the forest were significantly more likely to be depredated by BTS (Table 1), and this effect was most pronounced in the youngest age classes (Figure 4).
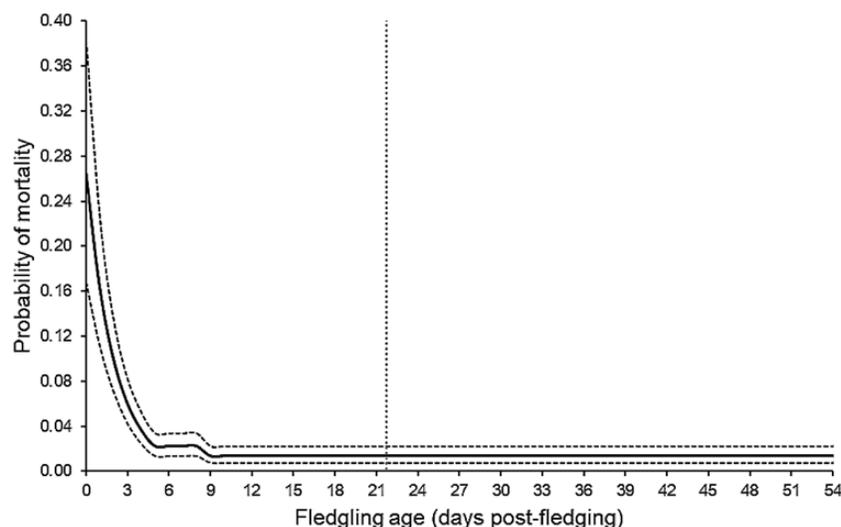

FIGURE 2. Daily probability of post-fledging mortality (mean ± 95% Bayesian Credible Intervals) in relation to fledgling age (*n* = 43). The dotted vertical line represents mean length of the post-fledging period (i.e. period before fledglings dispersed from natal territory).
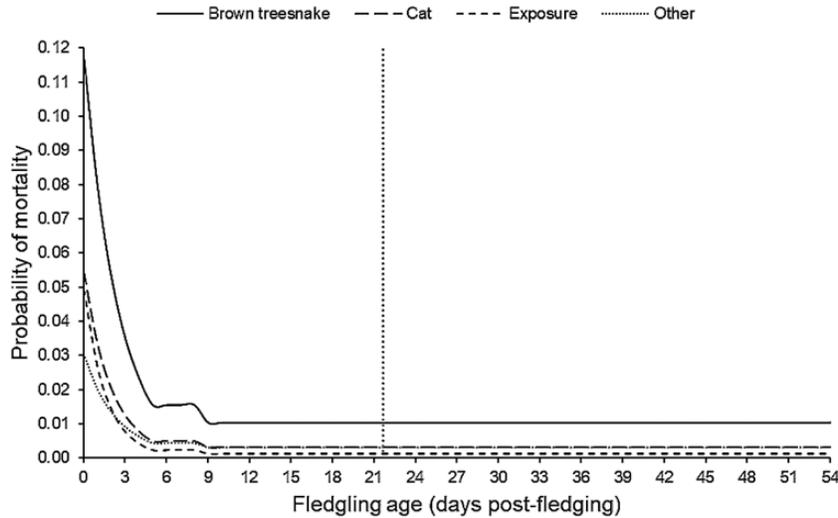
FIGURE 3. Cause-specific (brown treesnake, cat, exposure, other) daily probabilities of post-fledging mortality in relation to fledgling age (*n* = 43). The dotted vertical gray line represents mean length of the post-fledging period (i.e. period before fledglings dispersed from natal territory).

TABLE 1. Modeled effects of 6 covariates on daily cause-specific mortality rates (due to brown treesnake [BTS], cat, exposure, or other cause) during the post-fledging period (*n* = 43). The coefficient (β), standard deviation (SD), and 95% Bayesian credible intervals (BCIs) are shown for the effect of each covariate on each cause-specific rate of mortality. Each of the 6 models included a single covariate plus the additive effect of fledgling age based on the best-supported age structure (7 age classes: 0, 1, 2, 3, 4, 5–8, and 9+ days post-fledging). We considered effects with 95% BCIs that did not overlap zero to be biologically significant (indicated in boldface)

Covariate—Cause of mortality	β	SD	95% BCIs
Body mass—BTS	0.031	0.118	−0.206 to 0.258
Body mass—Cat	0.058	0.142	−0.225 to 0.333
Body mass—Exposure	0.002	0.013	−0.023 to 0.029
Body mass—Other	0.001	0.013	−0.024 to 0.026
Body size (tarsus)—BTS	0.045	0.112	−0.180 to 0.257
Body size (tarsus)—Cat	0.073	0.134	−0.192 to 0.335
Body size (tarsus)—Exposure	0.010	0.032	−0.053 to 0.073
Body size (tarsus)—Other	0.010	0.030	−0.049 to 0.069
Body condition (tarsus:mass residuals)—BTS	−0.016	0.100	−0.211 to 0.182
Body condition (tarsus:mass residuals)—Cat	−0.060	0.134	−0.318 to 0.206
Body condition (tarsus:mass residuals)—Exposure	−0.035	0.076	−0.180 to 0.115
Body condition (tarsus:mass residuals)—Other	−0.115	0.079	−0.267 to 0.045
Brood size—BTS	−0.041	0.127	−0.299 to 0.202
Brood size—Cat	0.072	0.150	−0.228 to 0.362
Brood size—Exposure	0.494	0.366	−0.228 to 1.211
Brood size—Other	0.244	0.366	−0.493 to 0.942
Fledge-date—BTS	0.123	0.121	−0.119 to 0.356
Fledge-date—Cat	0.065	0.150	−0.232 to 0.354
Fledge-date—Exposure	−0.001	0.004	−0.008 to 0.007
Fledge-date—Other	0.001	0.004	−0.006 to 0.008
Distance fledged from forest—BTS	**−0.280**	**0.141**	**−0.568 to −0.016**
Distance fledged from forest—Cat	−0.014	0.163	−0.347 to 0.293
Distance fledged from forest—Exposure	−0.001	0.002	−0.004 to 0.002
Distance fledged from forest—Other	−0.003	0.002	−0.006 to 0.000

Post-fledging Movement and Habitat Use

Fledglings remained within 100 m of natal nest boxes during the first 10 days post-fledging (Figure 5), and most mortality also occurred close to the natal nest box (≤150 m; Supplemental Material Figure S3). After 10 days, fledglings gradually moved farther from nest boxes, and eventually dispersed from their natal territories around 3 weeks post-fledging (21.7 ± 0.7 days; *n* = 14). Prior to natal dispersal, we recorded 334 diurnal resights and 107 nocturnal roost locations of fledglings, of which only 20 diurnal (6.0%) and
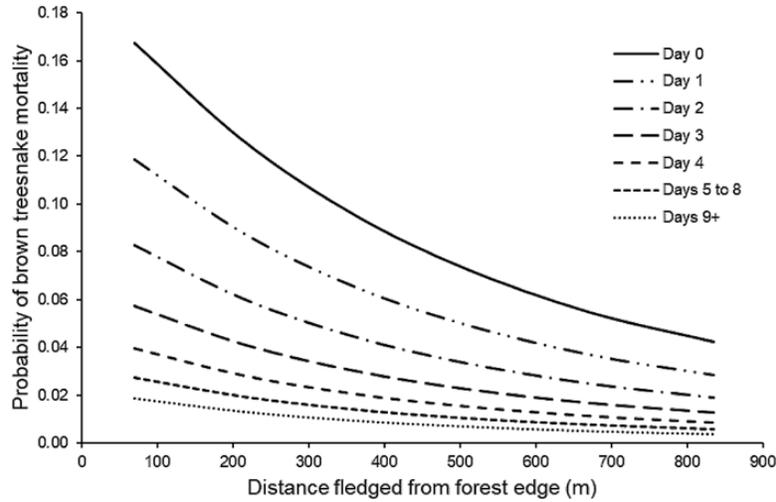
FIGURE 4. Probability of post-fledging mortality due to predation by brown treesnakes as a function of distance fledged from the forest edge for each age class.
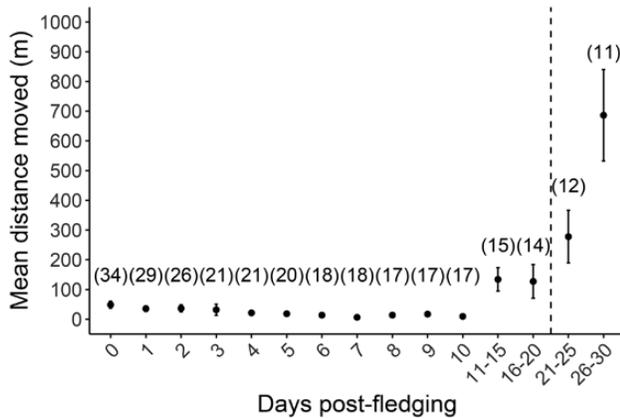

FIGURE 5. Mean distance moved from the natal nest box (±SE) for fledglings during and immediately after the post-fledging period. Sample sizes are indicated above each age class in parentheses. The dashed line indicates the mean length (21.7 days) of the post-fledging period (i.e. when fledglings dispersed from the natal territory).

3 nocturnal locations (2.8%) occurred in forest habitat. These 23 observations were associated with 6 fledglings, all of which died—4 due to BTS predation, 1 due to an unknown predator, and 1 due to unknown causes. These 6 fledglings started using forest significantly earlier in the post-fledging period (4.7 ± 1.5 days) than fledglings that survived (22.6 ± 0.8 days; $n = 11$; $t = 6.32$, df = 15, $P < 0.0001$).

DISCUSSION

We documented pervasive impacts of the introduced predatory BTS on the fledgling survival of Micronesian

Starlings, one of Guam's 2 remaining native forest bird species. BTS were the main source of fledgling mortality, accounting for ~56% of all deaths. Although predation is the primary source of fledgling mortality in most bird populations (Vitz and Rodewald 2011, Naef-Daenzer and Grüebler 2016), predation levels are particularly high in this system.

Post-fledging survival rates of 38% at 3 weeks post-fledging and 26% at 9 weeks post-fledging are among the lowest rates ever reported for passerine birds. In a review of 31 passerine post-fledging survival studies, Cox et al. (2014) reported only 4 studies concerning 3 species that found lower survival rates during the first 3 weeks post-fledging (range: 23–37%; Yackel-Adams et al. 2001, 2006; Fink 2003, Rush and Stutchbury 2008). All 3 species are either cup-nesting passerines (Lark Bunting [*Calamospiza melanocorys*], Hooded Warbler [*Setophaga citrina*]) or a brood parasite of cup-nesting passerines (Brown-headed Cowbird [*Molothrus ater*]) with short nestling periods (range: 8.5–10.5 days; Lowther 1993). As a result, their nestlings are less developed upon fledging and more susceptible to predators (Cox et al. 2014). In contrast, cavity-nesting species like Micronesian Starlings have longer nestling periods (i.e. 25 days; Jenkins 1983, M. Kastner personal observation). Therefore, they are more developed when they fledge and better able to evade predators, resulting in consistently higher fledgling survival rates (cavity nesters = 0.79, range 0.64–0.87, $n = 4$ species; cup nesters = 0.54, range 0.23–0.83, $n = 18$ species; Cox et al. 2014). These values contextualize the exceptionally low fledgling survival rate (i.e. only 34–47% of survival rates of other cavity nesters reviewed in Cox et al. 2014) of starlings on Guam, even relative to species from other island systems with introduced nocturnal predators (e.g., 79.5%

in Black-fronted Terns [*Chlidonias albostriatus*], Keedwell 2003; 57% in Seychelles Parrot [*Coracopsis barklyi*], Reauleaux et al. 2014; but see Moorhouse et al. 2003, 25–43% in New Zealand Kaka [*Nestor meridionalis*]).

Our cause-specific approach allowed us to model the probability of mortality by each source over time and revealed that predation by BTS extended beyond the post-fledging period and natal dispersal. Consistent with most post-fledging survival studies, we found that age was the best predictor of fledgling survival (Sullivan 1989, Weathers and Sullivan 1989, Yackel Adams et al. 2006, Cox et al. 2014, Naef-Daenzer and Grübler 2016, Jones et al. 2017b). The preponderance of mortality occurred early in the post-fledging period. Similarly, nearly all mortality by non-BTS sources (with the exception of one feral cat predation of a 33-day-old fledgling) occurred within the first 4 days post-fledging. In contrast, BTS predation persisted well beyond the post-fledging period (Figure 3). Five predation events occurred on fledglings >20 days old, including the depredation of a 53-day-old fledgling, resulting in an additional 12% reduction in fledgling survival (from 38% to 26%) between weeks 3 and 8 post-fledging. The ongoing elevated risk of predation by BTS beyond the post-fledging period is exceptional compared to most natural systems (Cox et al. 2014) and even other invaded island ecosystems, where probability of mortality declines to near zero after day 20 post-fledging in species such as the New Zealand Kaka (Dilks et al. 2003) and the Black-fronted Tern (Keedwell 2003). Nevertheless, mortality dropped to zero for all birds (*n* = 11) that survived beyond 53 days post-fledging (mean ± SD tracking duration = 116.5 ± 43.9 days), suggesting that older age classes (i.e. juveniles and adults) may have much higher survival rates that may be contributing to starling persistence on Guam.

Apart from fledgling age and predator identity, none of the factors that have typically been found to influence fledgling survival in other species had a significant impact in this system. For example, previous studies have found strong positive correlations between fledgling survival and body mass or condition (Suedkamp-Wells et al. 2007, Vitz and Rodewald 2011, Maness and Anderson 2013, Cox et al. 2014, Naef-Daenzer and Grüebler 2016; but see Streby et al. 2014), which can indicate that a fledgling's nutritional status may influence its ability to escape predators. Similarly, there is often a negative correlation between brood size and fledgling survival; fledglings from larger broods have reduced survival due to competition with siblings or reduced parental care (Tarof et al. 2011, Naef-Daenzer and Grüebler 2016). However, none of these predictor variables was correlated with fledgling survival in our system. We hypothesize that the impact of BTS may be masking or overriding associations typically found between phenotypic traits and fledgling survival rates. Because Micronesian Starlings did not coevolve with

nocturnal, arboreal predators such as BTS, traits that influence predation risk such as wing development (Martin 2014, Jones et al. 2017b, Martin et al. 2018) or parental care may not be as important for fledgling survival in our system. However, testing this hypothesis would require comparative data from a locality where BTS are absent to determine the influence of other phenotypic traits on fledgling survival.

Nest location was an important predictor of post-fledging survival. Fledglings tended to stay close to their urban nest boxes during the post-fledging period and rarely used the forest prior to natal dispersal, especially at night when BTS are active (i.e. only 2.8% of roosting observations). On the neighboring island of Saipan, which is free of BTS, Micronesian Starlings use a variety of habitats but are more abundant in forest (Jenkins 1983) and tend to select forest over other habitat types (Rehm et al. 2018). Therefore, the predominant use of urban habitat by starlings for nesting on Guam appears to be a behavioral adaptation to reduce, particularly for younger birds, the risk of predation from nocturnal BTS. Indeed, the 6 fledglings that were resighted in the forest prior to natal dispersal all died, and 4 of these were depredated by BTS. Additionally, these 6 birds began using forest at a significantly younger age than birds who survived, and all 6 fledged from nests within 150 m of the forest edge. More generally, we found a strong correlation between fledgling survival and nest location; birds that fledged from nests closer to forest were significantly more likely to be depredated by BTS. Taken together, these results indicate that nest location informs predation risk for young birds, a finding with important management implications.

Conservation Implications and Management Recommendations

Our study provides important baseline information on the demographic impacts of BTS and sheds light on the challenges of reintroducing extirpated native bird species on Guam. Despite ongoing snake control and removal efforts on Andersen Air Force Base, BTS continue to have a powerful impact on the starling population. For example, of the 18 BTS predation events, we estimate (based on observed timing and causes of death for all fledglings) that 13 (72%) of those deaths were additive, resulting in a 30% increase in overall fledgling mortality (from 44% to 74%). Nevertheless, the population has persisted and has grown in recent years (M. Kastner personal observation), suggesting that starlings may have other adaptations or strategies for coping with high predation risk. For example, starlings on Guam appear to have high adult survival (H. S. Pollock and M. Kastner personal observations) and high fecundity, with pairs often renesting throughout the year (J. A. Savidge personal observation), both of which probably help offset high fledgling mortality. Additionally, our

findings reveal several insights into how avian populations can survive in the face of this invasive predator. The importance of areas with low snake density for fledgling survival is the most obvious takeaway (see Wiles et al. 2003). A striking result was the increased vulnerability of birds that fledged from nest boxes closer to forest. Future efforts to expand the starling population should balance the utility of forest habitat for foraging with the elevated predation risk it poses to fledglings. If possible, we recommend placing nest boxes in urban areas at least 150 m away from the forest edge. This distance would allow adults, which are highly mobile, to easily access forest food resources while reducing fledgling predation risk by 25% or more. More broadly, our findings demonstrate the importance of taking habitat associations of invasive predators into account to maximize efficacy of conservation efforts.

Urban habitat clearly serves as a refuge from BTS predation, most likely due to a combination of snake control and snake behavior. BTS tend to avoid roads (Siers et al. 2014) and highly lit areas (Campbell et al. 2008), both of which typify urban areas on Andersen Air Force Base. Therefore, BTS abundance and predation risk could conceivably be lower on base relative to the surrounding forest, although habitat-specific BTS abundance data would be required to test this hypothesis. Regardless, tolerance to urbanization or access to urban roosting sites may be a prerequisite for persistence of avian populations in the presence of BTS. However, we stress that urban habitat is by no means "safe" habitat for fledgling birds. Most BTS predation events (72%) occurred in the urban area, indicating that snake control primarily around the base perimeter (along the forest–urban ecotone) is not sufficient for preventing snake incursions into the urban area. Furthermore, although we found no evidence that fledglings from the same nest box had correlated fates, we did observe several instances of BTS predation on fledglings from consecutive broods, suggesting that there may be an urban snake population systematically preying on starling fledglings (Wagner et al. 2018). Indeed, BTS on Guam often attain superior body condition and larger body size in urban habitats, which support a larger variety of vertebrate prey than forest habitats (Savidge 1991, Siers et al. 2017, Wagner et al. 2018). We therefore recommend exploring complementary control methods focused on suppressing BTS in urban areas.

Predation by feral cats was also an important source of mortality, resulting in 19% of all fledgling deaths. One individual cat was a serial predator, depredating fledglings that originated from the same nest box in consecutive broods (Supplemental Material Figure S2). Even a small number of feral cats has the potential to have a disproportionately large negative demographic impact on a prey population (Leo et al. 2018). Our results corroborate previous studies demonstrating that impacts of feral cats on island bird populations can be especially severe (Blackburn et al. 2004, Clavero et al. 2009, Jones and Merton 2012), and we echo the call of implementing cat control to increase the survival of native birds (Courchamp et al. 2003, Nogales et al. 2004). Although research on post-fledgling survival has increased in recent decades (Cox et al. 2014), few studies have addressed the impacts of invasive predators on this demographic parameter, particularly within island ecosystems (but see Dilks et al. 2003, Keedwell 2003, Moorhouse et al. 2003, Reauleaux et al. 2014). Our findings indicate that these impacts can be severe, yet we are optimistic that suppressing invasive predator populations and making informed conservation decisions (e.g., where to place nest boxes on the landscape) can facilitate the success of native birds on Guam and in other island ecosystems.

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