Nest success and life history syndromes of island and continental Rufous Fantail (*Rhipidura rufifrons*) subspecies

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A dissertation

submitted in partial fulfillment of the

requirements for the degree of

Doctor of Philosophy

University of Washington

2018

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Abstract

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Insular avian species are predicted to have slower life history syndromes than related continental species, due to lower predator diversity on oceanic islands. However, detailed studies of nest predation, life history and behavior of related oceanic island and continental taxa are lacking. I studied Rufous Fantail (*Rhipidura rufifrons*) life history traits in New South Wales, Australia and on the oceanic island of Rota, Commonwealth of the Northern Mariana Islands. Average daily survival rate (DSR) of nests was similar between sites, but this owed to a disordinal interaction between site and nest age. DSR was negatively related to nest age in Australia, likely because nest predation by reptiles usually occurred late in the nestling stage. By contrast, DSR was higher in the nestling stage than the egg stage on Rota. Nest site characteristics were unrelated to DSR at both sites and nest fate was not repeatable when fantails reused nest sites for multiple clutches. Therefore, nest predation may occur incidentally, rather than due to intrinsic

differences in nest site quality. As expected, insular fantails had a slower life history syndrome: fantails on Rota had longer nestling development periods, higher nestling provisioning rates and slower growth of nestling locomotor traits. At both sites, nest guarding effort decreased with increasing nestling provisioning rate, suggesting a trade-off between these activities. However, regardless of provisioning rate, fantails spent more time guarding their nests on Rota than in Australia. I could not compare adult survival between study sites because color bands caused leg injuries on Rota, while I did not observe band-related injuries in Australia. Site-specific differences in the prevalence of band-related injuries may reflect variation in the frequency with which fantails encounter spider webs, since injuries were caused by spider web accumulation under the bands. Overall, my results suggest that one causal explanation for life history differences between continental and insular birds is variation in age-dependent DSR due to reduced predator diversity on oceanic islands. Additionally, increased investment in offspring and slower development of nestling locomotor traits may explain some of the vulnerability of insular birds to the introduction of non-native predators.

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ACKNOWLEDGMENTS

My advisor, Renee Ha, provided tireless support and encouragement for the duration of my dissertation research. I would also like to thank my committee members Mike Beecher, Julie Savidge and Aaron Wirsing for their constructive feedback and thoughtful comments. Members of the Ha lab (Sarah Faegre, Saethra Fritscher, Carly Loyer, Anton Mates, Kelsey McCune, Adrian Sussman and Carol Xu) and the Animal Behavior Journal Club provided valuable discourse, especially during the planning stages of this project. Many people assisted with permitting and coordinating field work logistics: I am indebted to Lainie Berry, Benjamin Cox, David Drynan, Mark Fletcher, Shelly Kremer, Jill Liske-Clarke, Manuel Pangelinan, Paul Radley and Colleen Turnbull. In particular, logistical assistance from Greg Clancy facilitated my research in Australia. Christa Beckman, Michael Guppy, Sarah Guppy and Steve Tremont graciously shared their observations of Australian nest predators and band-related injuries in other Australian passerines. Andria Kroner provided Mariana Crow sightings data. Thomas Martin and Zhong Wang shared R code for the growth rate calculations. Dana Alexander, Yuchen Cao, Diane Danao, Mara Jacobo, Zhu Li and Madison Mariani coded feeding rate videos. Wenyi Zhou assisted with video coding as well as data analysis and editing for Chapter 3. Chris Adolph, Carol Bogesi, Sarah Faegre, Leith Leiser-Miller, Dave Slager and several anonymous reviewers provided peer-reviews that greatly improved the quality of my dissertation chapters. This project would not have been possible without funding from the National Science Foundation Graduate Research Fellowship, American Ornithologists' Union Student Research Award, Animal Behavior Society Student Research Grant, University of Washington (UW) Psychology Department Scholars Fellowship, UW Bolles Fellowship and UW Alcor Fellowship.

Finally, I am grateful for support from my family and friends. My parents, Ann Dougherty and Jim Nietmann, have always encouraged the traits that made this project possible: creativity, curiosity, attention to detail, perseverance and resilience. My parents also provided assistance with designing my infrared camera system, carving fantail decoys and procuring materials for making the pin-striped color bands. Adventures with my brother, Spencer Nietmann, and his partner, Katherine Creswell, always endowed me with a rejuvenated perspective. Finally, my partner, Aaron Cavagnolo, brightened the last two years of this experience with his humor, encouragement and support.

DEDICATION

In memory of Jeremy Hayward

1987 - 2015

Chapter 1: Variation in age-dependent nest predation between island and continental Rufous Fantail subspecies

INTRODUCTION

Animals are expected to shift toward a slower, more K-selected life history strategy following island colonization (MacArthur and Wilson 1967). Evidence for this 'island syndrome' in birds includes observations of smaller clutch sizes, increased investment per offspring and slower offspring development on islands relative to continents (Grant and Grant 1980, Crowell and Rothstein 1981, Bosque and Bosque 1995, Blondel 2000, Covas 2012). On most oceanic islands, the native nest predator community includes birds (predominantly passerines and near-passerines) but few mammals or reptiles. Age-specific mortality a major source of selection in avian life history evolution, and many life history traits show strong covariation with nest predation risk (Martin 1995, 2015). The low predator diversity on oceanic islands is believed to reduce nest predation rates on islands compared to continents, thereby explaining the longer nestling development periods of insular species (Bosque and Bosque 1995, Covas 2012).

However, there are several reasons to believe that nest predation risk is independent of nest predator diversity and that island birds may experience significant nest predation risk. First, species-depauperate communities may experience 'density compensation,' whereby low diversity is offset by high densities of the occurring species (MacArthur et al. 1972). Second, the absence of a specific predator guild does not necessarily translate to increased nest success, due to compensatory nest predation by other predator species (Ellis-Felege et al. 2012). Passerine and near-passerine birds are

common nest predators (e.g., Stevens et al. 2008, Guppy et al. 2017, Menezes and Marini 2017), suggesting that purely avian predator communities on oceanic islands could cause high nest predation rates. Third, a small subset of the suspected nest predator community is generally responsible for most predation events (Thompson and Burhans 2003, Weidinger 2009). Even in tropical forest, the majority of nest predation events are attributed to one or two predator species, despite the diversity of potential predators (Pierce and Pobrasert 2013, Visco and Sherry 2015). Indeed, nest predation risk can be unrelated to predator species richness (DeGregorio et al. 2016), while density and/or activity level of specific predators predicts nest predation rates in many systems (Zanette and Jenkins 2000, Luginbuhl et al. 2001, Roos 2002, Vigallon and Marzluff 2005).

Predator identity explains significant variation in nest predation risk both within and between study systems (Benson et al. 2010, DeGregorio et al. 2016). For example, some reptiles are frequent predators of nestling stage nests, presumably due to the olfactory and visual conspicuousness of nests containing large nestlings (Benson et al. 2010, Cox et al. 2012, Reidy and Thompson 2012). Raptors also tend to prey upon nestlings (Benson et al. 2010, Cox et al. 2012, Pierce and Pobprasert 2013), whereas smaller-bodied avian predators prey upon eggs more often than nestlings (Stake et al. 2004, Weidinger 2009, Benson et al. 2010, Rodewald and Kearns 2011, Guppy et al. 2017) . Nest-site characteristics such as height and concealment predict predation risk by passerine and near-passerine predators (Santisteban et al. 2002, Remeš 2005, Benson et al. 2010), suggesting that these predators detect nests by visual searching. Indeed, nest site quality predicts predation risk during incubation, whereas parental activity is related to nestling stage predation rates (Martin et al. 2000). By implication, the foraging

modality of the principal predators influences stage-specific predation risk. Therefore, lower nestling stage predation rates due to variation in predator community composition could relax selection on nestling development period length. This effect could be independent of average nest predation rates—which are potentially skewed by incubation-stage predation—because evidence suggests that certain predators may target nestling stage nests more frequently than incubation-stage nests (e.g., Benson et al. 2010).

Previously, small sample sizes and reporting of apparent nest success rather than daily survival rates on islands have precluded the comparison of nest predation rates between taxonomically related island and continental species (Covas 2012). Here I present results from the first direct comparison of continental and oceanic island nest predation rates, using Rufous Fantails (*Rhipidura rufifrons,* hereafter 'fantails') as a model system. Fantails at my island site (Rota, Commonwealth of the Northern Mariana Islands, hereafter 'Rota'), have a longer nestling period (12.71 ± 0.13 days) than at my continental site (Iluka, NSW, Australia, hereafter 'Australia;'11.57 ± 0.17 days, Chapter 2), suggesting that this system is representative of the general pattern of longer developmental periods on islands (e.g., Bosque and Bosque 1995, Covas 2012). I predicted that the predominantly passerine nest predator community on Rota would be related to an increase in daily survival rate with nest age whereas the occurrence of reptiles and raptors in Australia would result in a decrease in daily survival rate with nest age.

METHODS

Study System

Fantails are 8-10 g forest passerines found throughout Western Oceania. They place their cup nests in shrubs or sub-canopy trees and both sexes participate in incubation, brooding and provisioning nestlings. Nests are placed 0.92 – 10.0 m (mean = 4.09 m) above ground in Australia and 0.45 – 4.34 m (1.59 m) above ground on Rota, a difference that likely reflects the taller canopy and sparser shrub layer in Australia (Chapter 3). At both sites, pairs generally nest in the same territory each year. In Australia, I studied fantails (*R. r. rufifrons*) September – January (2014 – 2016) in Iluka Nature Reserve (29.4058°S, 153.3601°E), an 88-ha stand of littoral rainforest that is part of the Gondwana Rainforests World Heritage Area. At this site, fantails breed between September and February (Higgins et al. 2006), before migrating to the northern tropics. This site receives an average of 1464 mm of rain per year, most of which falls between December and March, and experiences a sub-tropical climate with average summer temperatures of 20 – 26 ºC (Grantley 2010).

On Rota, I studied fantails (*R. r. mariae*) March – June (2013 – 2015 and 2017) at two different sites on public land in Tatgua (14.1776°N, 145.2067°E) and Koridot (14.1554°N, 145.2499°E). I chose to work on two plots due to the limited availability of large, contiguous and easily accessible native forest patches. Fantails breed year-round on Rota, with reported peaks in nesting activity February – May and September – November (Pyle et al. 2008). The climate on Rota is tropical with year-round high temperatures averaging 28 – 30 ºC. Most of the 2440 mm of annual rainfall occurs between July and December (NOAA 2017). The only native nest predators on Rota are passerine and near-passerine birds. Rats (*Rattus* spp.) and Black Drongos (*Dicrurus macrocercus*) have been introduced (Baker 1951, Steadman 1999). Mangrove monitor lizards (*Varanus indicus*)

also occur on Rota, although the origin of the population is debated (Steadman 1999, Cota 2008, Pregill and Steadman 2009).

Nest Monitoring

I located nests by observing behavior of each breeding pair and marked nest locations by flagging a tree at least 5 m from the nest. I checked nest contents every 2 – 4 days, with checks occurring daily or twice daily around hatching and fledging to confirm nestling period lengths. To avoid attracting predators to the nest, I performed a brief visual and auditory scan of the area for predators prior to checking each nest. I also did several "dummy checks" as I approached and retreated from the nest, which involved peering into random sites as if checking a nest. Nests located above my reach were checked using a small mirror mounted on a pole. When possible, I confirmed nest contents based on observations of fantail nest attendance rather than approaching the nest.

Any nestlings that disappeared more than two days before the modal fledging age (11 days in Australia and 13 days on Rota) were considered preyed upon. If the nest was found empty within two days of expected fledging, I searched the area for fledglings. If the adults (identified by color bands and/or territory occupancy) were located without fledglings and/or were found building a new nest, I considered the nest preyed upon. Video recordings corroborated these assumptions—nestlings did not successfully fledge before 10 days in Australia and 11 (usually 12 or 13) days on Rota. Using these rules, I correctly identified nest fate for 29 of 30 video-recorded fates during the two days prior to fledging. While it is possible that starvation or disease caused nestling mortality, other studies have found that nest predation is the predominate source of nestling mortality in passerine birds (Benson et al. 2010, Cox et al. 2012, Reidy and Thompson 2012).

Nest Cameras

I used two types of infrared (IR) cameras to identify nest predators in 2015 and 2016 in Australia and in 2017 on Rota. To record predation events in real time, I used infrared cameras (Interlogix, Costa Mesa, California, USA) connected to single channel DVRs (Supercircuits, Austin, Texas, USA) and powered by 12V deep cycle batteries. Cameras were placed 1 – 2 m from nests and connected to DVRs and batteries via 6 m of cable, so that batteries and memory cards could be changed without disturbing the nest. Cameras were covered in camouflaged duct tape and disguised with vegetation. I placed IR cameras at least 3 days after clutch completion to minimize disturbance and confirmed that fantails resumed a normal incubation rhythm within 20 min of camera placement. I visited nests every other day to replace the memory card and every four days to replace the battery. I also used five MP6 passive infrared (PIR) cameras (Covert Scouting Cameras, Lewisburg, Kentucky, USA), which took still-frame photographs when the sensor was triggered (hereafter 'PIR cameras'). PIR cameras were placed 1 – 3 m from the nest with the field of view centered on the nest. I set PIR cameras to high sensitivity and programed them to take three photos following each trigger (trigger speed = 1.2 s, trigger interval = 5 s). Cameras were checked during normally scheduled nest checks (i.e. every 2-4 days).

Climate Data

Annual rainfall patterns predict variation in the number of hatch year fantails captured on the island of Saipan (115 km from Rota, Saracco et al. 2016), likely reflecting an effect of rainfall on nest success and/or post-fledging survival. Therefore, I included climatic

variables in my models of nest success for both sites. I used daily temperature and precipitation data collected at the Yamba Pilot Station (3.0 km from my study site in Australia, Bureau of Meteorology 2017) and at the Rota Airport (2.0 and 4.1 km from my study plots in Koridot and Tatgua, respectively; NOAA 2017). The Rota Airport reported data for only 60% of the days included in my study, so I substituted data for missing values from the weather station at the Guam Airport (90 km from Rota, NOAA 2017). Guam and Rota experience similar annual average temperatures and rainfall (Rogers et al. 2012). For each nest, I calculated average daily rainfall for the duration the nest was active (hereafter 'daily rain'). For each interval between nest checks, I calculated average high temperature and average daily rainfall (hereafter 'high temperature' and 'interval rain,' respectively). For these latter measures, I was interested in whether broad climatic patterns influenced nest predation rates by influencing predator activity rates. Therefore, I converted interval rain into a simple rating scale: no rain (0mm/day), some rain (≤10mm/day), or significant rain (>10mm/day).

Data Analysis

I modelled daily survival rate (DSR) of fantail nests by fitting logistic exposure models in R 3.4.2 (Shaffer 2004, R Core Team 2017). Nests that were abandoned (N = 10) were not included in my analysis. I then used an information-theoretic approach (Burnham et al. 2011) to evaluate the relationship between various covariates and DSR. To avoid the inclusion of models containing uninformative parameters in my candidate model sets, I only considered a model to be a candidate for inference if it was ranked within 4 ΔAIC_c and was not nested within or above the top-ranked model (Arnold 2010). Using this procedure, I selected only the top-ranked model from each model set to use for inference.

I corroborated the exclusion of alternative models by confirming that the 85% confidence intervals of the estimates for parameters present in competitive models (< 4 ΔAIC_c) overlapped zero (Arnold 2010). To describe differences in nest survival between Rota and Australia, I compared four candidate models including additive effects of nest age (days after clutch initiation) and site as well as site-specific age effects (i.e. the interaction between site and age, Appendix Table A1.1). I then examined stage-specific differences between sites by modelling DSR separately for egg (laying and incubation) and nestling stage nests with site as a single fixed effect.

I then modelled nest survival separately for Australia and Rota, because I had different a priori hypotheses about the relationship between nest success and various fixed effects at each site. Prior to formulating candidate models for each site, I determined whether DSR would best be modelled with nest age as a continuous variable ('age,' i.e. days after clutch initiation) or a categorical variable ('stage,' i.e. egg vs. nestling) by comparing AIC_c weights (Burnham et al. 2011) of models containing each of these parameters separately for each site. Next, I fit a constant survival (i.e. intercept-only) model for each site to facilitate inclusion of my DSR estimates in future comparative studies. To model DSR in Australia, I fit 43 candidate models containing hypothesis-driven permutations of the fixed effects year, age, day of year, camera presence, the three climate variables described above, a quadratic effect of age, and the interaction between year and age (Appendix Table A1.2). To model DSR on Rota, I evaluated 42 candidate models containing hypothesis-driven permutations of the fixed effects year, stage, plot, day of year, camera presence, the three climate variables described above, and interactions of both plot and year with stage (Appendix Table

A1.3).

For nests in Australia, I used multinomial logistic regression (Venables and Ripley 2002) to determine whether climate influenced predator-specific predation risk. I used cameras to determine the date of predation by birds or monitor lizards and cameras or twice-daily nest checks to determine the date of fledging. For these dates, I noted the high temperature and whether rain was recorded that day from the climate dataset described above. Because the focus of this analysis was on the degree to which weather influenced a predator's discovery of a nest, I coded six instances where predators (five monitor lizards and one bird) caused force-fledging as preyed upon, rather than fledged. I also counted two instances of a predator stealing only one egg (i.e. 'partial predation') as predation events. I excluded nests from 2014 a priori because I only had data from fledged nests and wanted to avoid biasing the data due to potential inter-annual variation in climate patterns. I performed a similar analysis for nests on Rota in 2017, but used binomial logistic regression to compare weather between days a nest fledged or was discovered by an avian predator.

RESULTS

I monitored 314 nests over 5826 observation days in Australia and 307 nests over 4574 observation days on Rota. Predation was the most common cause of nest failure at both sites (Table 1.1). The constant survival estimates of DSR were similar between Australia (0.967, 95% CI = 0.962, 0.972) and Rota (0.963, 95% CI = 0.958, 0.969). For both sites combined, the multiplicative model including fixed effects of site and age received 100% of the AIC_c weight (Appendix Table A1.1). The relationship between age and DSR

depended on site (Fig. 1.1, Table 1.2). Nests in Australia experienced a decline in DSR with age and nests on Rota experienced constant—or possibly increasing—DSR with age (Fig. 1.1), which explains the similarity in constant survival DSR between sites. On average, egg stage DSR was higher in Australia (0.980, 95% CI = 0.975, 0.985) than on Rota (0.962, 95% CI = 0.953, 0.969), while nestling stage DSR was higher on Rota (0.978, 95% CI = 0.969, 0.983) than in Australia (0.953, 95% CI = 0.943, 0.961).

Australia

In Australia, the model containing the continuous variable 'age' received 100% of the AIC_c weight, compared to the model containing the categorical variable 'stage,' therefore I used 'age' in subsequent analyses. The multiplicative model including age and year received the most support (Appendix Table A1.2). In all years, DSR declined with age, although there was marginal support for a more gradual decline in 2015 than in 2014 or 2016 (Table 1.2, Fig. 1.1B). Model predictions of DSR were higher in 2014 (0.982, 95% CI = 0.973, 0.988) than in 2015 (0.973, 95% CI = 0.964, 0.980) or 2016 (0.967, 95% CI = 0.957, 0.974; Table 1.2, Fig. 1.1B). Neither day of year, camera presence, nor any of the climate variables predicted DSR (Appendix Table A1.4). Lace monitors (*Varanus varius*) and a diversity of avian predators were responsible for the majority of predation events (Table 1.1). Of the 12 lace monitor predation events I observed, 10 (83%) happened during the nestling stage (Fig. 1.2). In addition, of the 11 fledging events I recorded with a camera, six (55%) were caused by a predator approaching the nest (five by lace monitors and one by a Lewin's Honeyeater, *Meliphaga lewinii*). Although weather did not influence overall DSR, climate did influence predator-specific nest survival probabilities. Lace monitors were less likely to discover a nest on a day with rain

(β = -2.18, 95% CI = -4.34, -0.03; Fig. 1.3), but there was no effect of temperature (β = 0.17, 95% CI = -0.12, 0.46). Neither rain (β = -0.44, 95% CI = -1.87, 0.99) nor temperature (β = -0.24, 95% CI = -0.56, 0.07) was related to the probability of an avian predator discovering a nest.

Rota

On Rota, the model containing the categorical variable 'stage' received 95% of the AIC_c weight, compared to the model containing the continuous variable 'age,' thus I used 'stage' in subsequent analyses. The additive model including plot and stage received the most support (Appendix Table A1.3). Nests in Tatgua had higher DSR (0.985, 95% CI = 0.978, 0.989) than nests in Koridot (0.959, 95% CI = 0.950, 0.967) and nestling stage nests had higher DSR (0.980, 95% CI = 0.972, 0.985) than egg stage nests (0.969, 95% CI = 0.961, 0.975; Table 1.2; Fig. 1.4). Mariana Crows (*Corvus kubaryi*) and non-native rats were the most commonly detected nest predators (Table 1.1). Neither day of year, camera presence, nor any of the climate variables predicted DSR (Appendix Table A1.5). High temperature (β = 0.15, 95% CI: -0.85, 1.22) and rain (β = -1.33, 95% CI: -3.11, 0.24) were unrelated to the probability of predation by birds.

DISCUSSION

Contrary to the assumption that nest predation risk is higher on continents than on oceanic islands (Bosque and Bosque 1995, Covas 2012), I found no difference in overall DSR between Australia and Rota. However, consideration of nest age revealed a critical difference in nest predation risk between my island and continental study sites. DSR declined significantly with age in Australia, while DSR increased during the nestling

stage relative to the egg stage on Rota. Additionally, egg stage DSR was higher in Australia than on Rota, whereas nestling stage DSR was higher on Rota than in Australia. Variation in nest predator community composition between my study sites likely explains this difference in stage-specific nest predation. For example, reptiles, raptors and kookaburras generally preyed upon nestlings in Australia, whereas Mariana Crows preyed upon eggs more often than nestlings on Rota (Table 1.1).

These results offer a more nuanced explanation for the longer nestling periods of species in Hawaii and New Zealand as compared to North America and Australia, respectively, as described by Bosque and Bosque (1995). Historically, islands hosted high densities of forest passerines (e.g., Hawaiian honeycreepers, Scott et al. 1986), many of which were likely nest predators given the prevalence of nest predation by passerine and near-passerine species in other systems (Stake et al. 2004, Stevens et al. 2008, Benson et al. 2010, Rodewald and Kearns 2011, Guppy et al. 2017). Native raptors occur in both Hawaii and New Zealand, but the low diversity of carnivorous reptiles (tuatara, *Sphenodon* spp., in New Zealand, no reptilian predators in Hawaii) may contribute to the life history differences between island and continental birds. Interestingly, Covas (2012) found no difference in the proportion of nests that were successful between island and continental birds. While such estimates are crude (i.e. not controlling for exposure period, taxonomy or predation by non-native predators), an alternative explanation is that this result reflects similarity in average predation rates, which may mask differences in stage-specific predation rates between islands and continents (e.g., Fig. 1.1).

Determining whether historical DSR was lower on continents than on islands is complicated by the high present-day densities of exotic predators on many islands (Covas

2012). For example, of the 16 predation events I observed on Rota, six (38%) were by non-native predators (Table 1.1), indicating that contemporary DSR may be artificially low. Indeed, nest success of many forest birds in New Zealand and Hawaii is substantially higher in environments lacking non-native predators (Vanderwerf 2009, Innes et al. 2010, Remeš et al. 2012). On Rota, two native nest predators on Rota, the Collared Kingfisher (*Todiramphus chloris*) and the Mariana Crow, have declined by 46% and 95% since 1982, respectively (Camp et al. 2015), and anecdotal observations suggest the Mariana Crow population was in decline prior to the start of formal surveys (Jenkins 1983). Despite their low population density, Mariana Crows were the most frequently recorded nest predator on Rota (Table 1.1, 56% of all recorded predation events), and the decrease in their population has surely increased fantail DSR. Therefore, it remains unclear whether contemporary DSR on Rota mirrors historic levels. However, based on the historically high densities of native avian predators, it is likely that forest bird species on Rota have never experienced the relaxation of average DSR that is commonly thought to characterize the life histories of oceanic island birds (Bosque and Bosque 1995). Additionally, the observation that non-native rats and Black Drongos collectively preyed upon equal numbers of egg (N = 3) and nestling (N = 3) stage nests (Table 1.1), suggests that the stage-specific differences in DSR on Rota would be similar, if not stronger, in the absence of non-native predators.

The longer nestling development period of fantails on Rota could result from a 'slower' life history syndrome at lower latitudes for reasons independent of nest predation risk (Martin 1996). For example, differences in breeding seasonality, parental investment, adult survival and food availability could explain differences in life history

traits between my study sites and should be explored in future studies. Mean and modal clutch size (2 eggs) is the same at both study sites and food delivery rate is greater on Rota than in Australia (Chapter 2). Therefore, elevated nestling stage nest attendance does not appear to be attracting predators to nests in Australia and instead nest predation may cause reduced nest attendance (Martin et al. 2000). Bosque and Bosque (1995) found that island cup nesting birds had longer nestling periods than their continental relatives, whereas there was no difference in nestling period length between island and continental cavity nesting birds. Since cup nests generally experience higher nest predation rates than cavity nests (Martin 1995), this implies that nest predation is an important selective agent driving life history differences between island and continental birds. Regardless, future studies should consider alternative explanations for my results, including whether the search effort of nest predators differed between my study sites due to breeding status or availability of alternative prey.

Among nests at my Australian site, I attribute the decline of DSR with age to lace monitor predation. Lace monitors tended to prey upon nests with large nestlings (Fig. 1.4), possibly because fantail nestling fecal material starts accumulating on the ground below the nest beginning ~7-8 days after hatching (personal observation). This may cue lace monitors to nest locations, because these predators primarily forage from the ground and use olfaction to locate prey (Cooper 1995, King and Green 1999). I found that lace monitor predation was less likely to occur on days when rain was recorded, presumably due to climate-dependent foraging activity (Guarino 2002) and/or attenuated olfactory cues following rain (Whelan et al. 1994). This relationship may explain the variation among years in the slope of the age-survival function (Fig. 1.1B). In 2015—the breeding

season with the smallest magnitude slope—rain was recorded on 50% of days, in contrast with 35% of days in 2014 and 27% of days in 2016, when I observed the most negatively sloping age-survival function. This result, although qualitative, suggests that the behavior of specific predators may mediate the relationship between seasonal climate trends and nest survival. Eastern Australia faces an uncertain future with respect to the effects of climate change on seasonal rainfall (Grose et al. 2015), therefore wildlife managers should consider the possibility that drier breeding seasons may reduce the productivity of cup-nesting passerines by elevating the risk of predation by reptiles.

On Rota, stage and plot were the most important predictors of DSR. Neither year of study nor any climatic variable predicted DSR, which suggests that post-fledging survival rather than nest success likely drives the inter-annual variability in capture rates of hatch-year fantails on the nearby island of Saipan (Saracco et al. 2016). DSR was lower for egg than nestling stage nests on Rota (Fig. 1.3), consistent with my prediction that a predominantly passerine nest predator community would be associated with higher predation rates early in the nesting cycle. While mean and modal incubation period length was 15 days at both sites (L. Nietmann, unpublished data), whether fantails on Rota compensate for the higher egg stage predation through behavioral modification (e.g. incubation prior to clutch completion and/or reduced nest visitation rates) compared to Australia should be examined by future studies.

A separate study on Saipan did not find an effect of stage on fantail DSR, despite similar constant survival (0.967, 95% CI = 0.956, 0.975; Sachtleben 2005) as I observed on Rota. While these islands are ecologically similar, neither Mariana Crows nor non-native Black Drongos occur on Saipan, suggesting that either or both of these predators

could drive the stage-specific predation rates I observed. Although I only observed Black Drongos taking fantail nestlings, Mariana Crows frequently preyed upon fantail eggs, indicating efficiency at exploiting nests early in the nesting cycle. Therefore, I believe that predation by Mariana Crows may explain the stage-specific differences in DSR on Rota. Mariana Crows may also cause the difference in DSR between my study plots on Rota (Fig. 1.3), since corvid density and activity are correlated with nest predation rates in other systems (Luginbuhl et al. 2001, Roos 2002, Vigallon and Marzluff 2005). A separate study controlling for search effort (Kroner and Ha 2017) detected an average of 0.19 Mariana Crows per hour in Tatgua and 0.89 Mariana Crows per hour in Koridot, corresponding to my observation of lower fantail DSR in Koridot.

Although corvids—including Mariana Crows—are capable of taking nestlings, other corvid species are also known to prey upon eggs more often than nestlings (Rodewald and Kearns 2011, Stake et al. 2004, Weidinger 2009). This could be because corvids locate nests incidentally or by visual searching (Santisteban et al. 2002, Vigallon and Marzluff 2005) and thus the most vulnerable nest sites may be discovered during incubation (e.g. Martin et al. 2000). Mariana Crows are primarily insectivorous (Faegre 2017), and they appear to find fantail nests while searching for other prey items (personal observation). Alternatively, corvids could use spatial memory to locate nests (Sonerud and Fjeld 1987). For example, Mariana Crows may discover nests based on fantails' conspicuous nest-building behavior and then re-visit nests following clutch initiation. Since Mariana Crows have large home ranges that overlap considerably with neighbors (Faegre et al. *In review*) as well as other nest predators, returning to consume nest contents early in the nesting cycle may be a competitive strategy. Finally, it is possible

that the high rate of nestling stage nest-guarding by fantails on Rota (Chapter 2) effectively deters Mariana Crows, especially since the availability of alternative prey on Rota is high (Faegre 2017).

Conclusion

My observations support a novel hypothesis to explain variation in life history traits between island and continental birds. The increasing risk of predation with age (Fig. 1.1B), combined with the elevated rate of force-fledging events at my Australian study site suggests that predators—especially reptiles—may exert a strong influence on developmental rates of nestlings in some continental systems. In contrast, the absence of nest predation by reptiles (and in some cases large birds) on many oceanic islands may result in lower predation pressure during the final days of the nestling stage. Thus relaxed selection on nestling period length in insular birds could arise from lower nest predator diversity, rather than an overall reduction in predation risk, as previously thought (Bosque and Bosque 1995, Covas 2012). I advise that future comparative studies consider stage-specific (or age-specific) DSR, given the potential for overall DSR to mask important differences in predation risk (e.g., Fig. 1.1). Future studies should: 1) consider the importance of predator community composition in influencing age-dependent nest predation rates in other systems and 2) investigate the effects of age-dependent nest predation risk on life history evolution in island and continental birds.

FIGURES

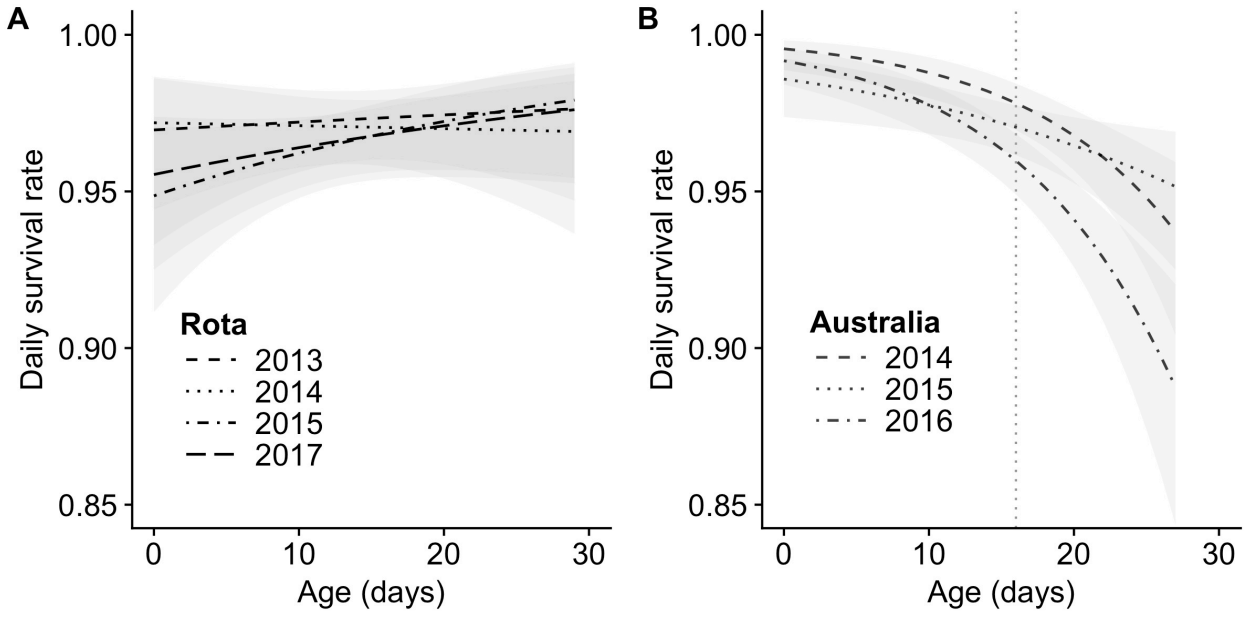

Figure 1.1 Daily survival rate of Rufous Fantail nests is relatively constant on Rota (A), but decreases significantly with nest age in Australia (B). Note that the modal fledging age in Australia is earlier (age = 27-28 days) than on Rota (age = 29 days), but eggs at both sites hatch 16 days (vertical dotted line) after clutch initiation (day 0). Shaded areas show 95% confidence intervals around model predictions for each year.

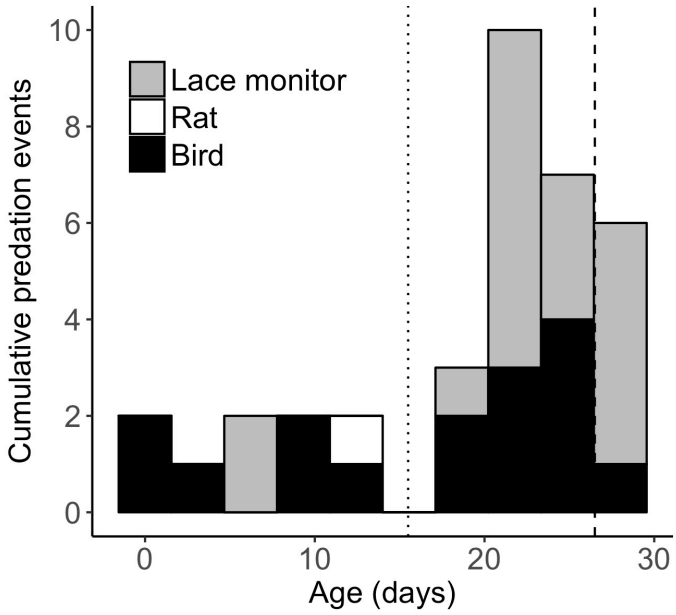

Figure 1.2. In Australia, infrared cameras reveal that lace monitors tend to prey upon nests later in the nestling stage, whereas avian predation occurs throughout the nesting cycle. The dotted line at x = 16 marks the modal hatching age and the dashed line at x = 27 marks the modal fledging age (i.e. observations to the right of the dashed line are force-fledging events).

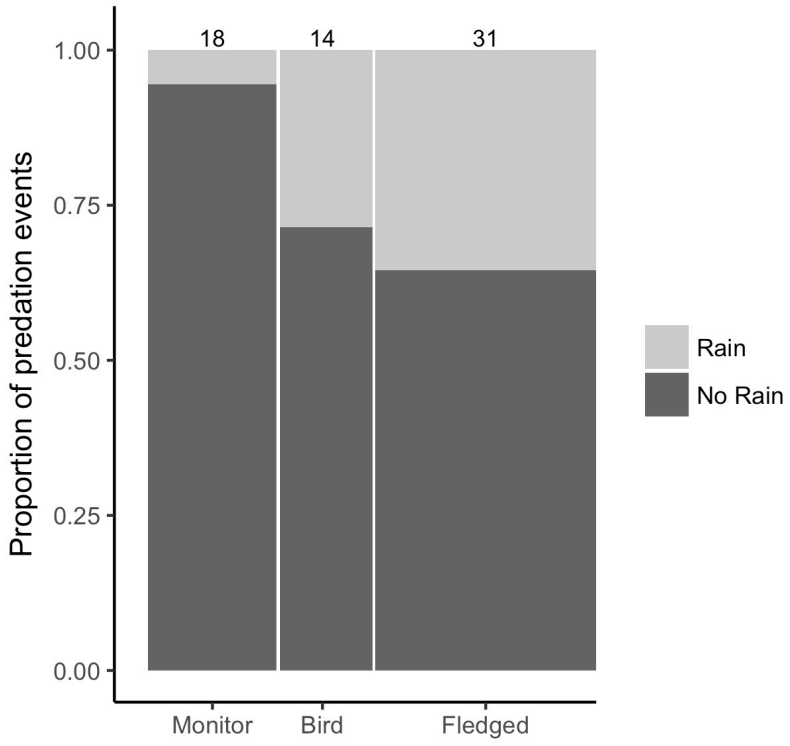

Figure 1.3. Proportion of nests in Australia that fledged or were preyed upon by birds or lace monitors on days rain was recorded at a nearby weather station or days rain was not recorded. Bar width is scaled to reflect sample size (indicated above bars).

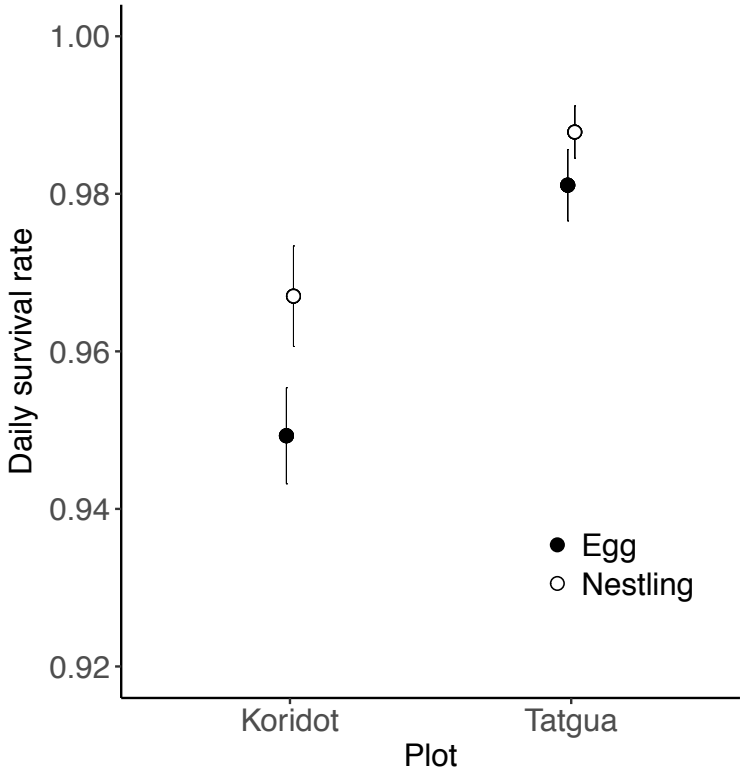

Figure 1.4. Daily survival rates (model predictions ± SE) of Rufous Fantail nests on Rota are higher in Tatgua than in Koridot and are higher during the nestling stage than during the egg stage (laying and incubation). Note that points have been offset to show error bar overlap.

TABLES

Table 1.1. Summary of Rufous Fantail nest failures (E = egg stage, N = nestling stage, FF = force-fledge) in Australia and Rota as determined by continuous video recording ('Video') or passive infrared cameras ('PIR camera').

		Video			PIR camera			
Australia		E	N	FF	E	N	FF	Total[a]
Predators	Lace monitor (*Varanus varius*)		3	4	2	7	1	18[b]
	Lewin's Honeyeater (*Meliphaga lewinii*)	1[c]		1	2			4
	Laughing Kookaburra (*Dacelo novaeguineae*)		3					3
	Brown Goshawk (*Accipiter fasciatus*)				1	1		2
	Pied Currawong (*Strepera graculina*)				1	1		2
	Regent Bowerbird (*Sericulus chrysocephalus*)		2					2
	Varied Triller (*Lalage leucomela*)		1					1
	Unknown bird[d]	1[c]						1
	Rat (*Rattus sp.*)	1						1
	Grey Goshawk (*Accipiter Novaehollandiae*)		1					1
Other failure	Camera malfunction	1	1		12	4		18
	Abandoned	1						1
	Nestling death		1					1
Rota								
Predators	Mariana Crow (*Corvus kubaryi*)	3			3	3		9
	Rat (*Rattus sp.*)[e]	2			1[c]	1		4
	Black Drongo (*Dicrurus macrocercus*)[e]		2[f]					2
	Collared Kingfisher (*Todiramphus chloris*)		1					1
Other failure	Camera malfunction				4	1		5
	Abandoned	1						1
	Nestling death		1					1

[a]Sum of independent events documented by each camera type
[b]Total includes one predation event witnessed incidentally during routine field work
[c]Partial predation
[d]Predator approximately the size of a Little Shrike-Thrush (*Colluricincla megarhyncha*)
[e]Non-native predator
[f]One partial and one complete predation

Table 1.2. Parameter estimates from logistic exposure models of Rufous Fantail nest survival at both sites (Overall), on Rota, and in Australia. Estimates are from the top-ranked model for each candidate set.

	Fixed effect	Estimate	SE	95% CI[1]
Overall[2]	Site*Age	0.10	0.02	**{0.067, 0.127}**
	Site	-1.52	0.27	**{-2.05, -1.01}**
	Age	-0.08	0.01	**{-0.10, -0.06}**
Rota	Plot	1.02	0.21	**{0.62, 1.45}**
	Stage	0.45	0.19	**{0.08, 0.84}**
Australia[3]	Age*Year2016	-0.05	0.02	**{-0.10, -0.01}**
	Age*Year2014	-0.05	0.03	{-0.11, 0.001}
	Age	-0.04	0.02	**{-0.08, -0.01}**
	Year2016	0.54	0.46	{-0.37, 1.45}
	Year2014	1.17	0.57	**{0.08, 2.33}**

[1]Values in bold indicate a 95% CI that does not overlap zero.

[2]Reference level for 'Site' set to Australia.

[3]Reference level for 'Year' set to 2015.

APPENDIX

Table A1.1. Candidate models for overall daily survival rate of Rufous Fantails nests.

Fixed effects	**K**	**ΔAIC_c[1]**	**w_i**	**LL**
Site*Age	4	0.00	1.00	-1059.07
Age	2	38.27	0.00	-1080.21
Site+Age	3	40.25	0.00	-1080.20
Null	1	55.99	0.00	-1090.07
Site	3	57.92	0.00	-1090.03

K = number of model parameters, ΔAIC_c = AIC_c distance from top-ranked model, w_i = Akaike weight, LL = log-likelihood

[1]Top-ranked model AIC_c = 2126.15

Table A1.2. Candidate models for daily survival rate of Rufous Fantail nests in Australia.

Fixed effects	**K**	**ΔAIC_c[1]**	**w_i[2]**	**LL**
age*year	6	0.00	0.15	-584.85
age*year + camera	7	0.68	0.11	-584.19
age*year + daily rain	7	0.80	0.10	-584.24
age*year + interval rain	7	1.01	0.09	-584.35
age + year	4	1.71	0.07	-587.71
age*year + high temperature	7	1.90	0.06	-584.79
age*year + day of year	7	1.92	0.06	-584.80
age + year + camera	5	2.35	0.05	-587.03
age + year + daily rain	5	2.57	0.04	-587.14
age + year + interval rain	5	2.70	0.04	-587.20
age^2 + year	5	3.26	0.03	-587.49
age + year + day of year	5	3.53	0.03	-587.62
age + year + high temperature	5	3.69	0.02	-587.70
age^2 + year + camera	6	3.70	0.02	-586.70
age + camera	3	3.93	0.02	-589.82
age^2 + year + daily rain	6	4.11	0.02	-586.90
age^2 + year + interval rain	6	4.26	0.02	-586.98
age^2 + year + day of year	6	5.09	0.01	-587.40
age^2 + camera	4	5.19	0.01	-589.45
age^2 + year + high temperature	6	5.24	0.01	-587.47
age^2*year	9	5.75	0.01	-584.71
age + daily rain	3	6.04	0.01	-590.88

K = number of model parameters, ΔAIC_c = AIC_c distance from top-ranked model, w_i = Akaike weight, LL = log-likelihood

[1]Top-ranked model AIC_c = 1181.73

[2]Models with $w_i < 0.01$ not shown

Table A1.3. Candidate models for daily survival rate of Rufous Fantail nests on Rota

Fixed effects	**K**	**ΔAIC_c[1]**	**w_i[2]**	**LL**
stage + plot	3	0.00	0.17	-450.10
stage + plot + daily rain	4	0.60	0.12	-449.40
stage*plot	4	1.28	0.09	-449.73
stage + plot + camera	4	1.46	0.08	-449.82
stage + plot + interval rain	4	1.62	0.07	-449.90
stage*plot + daily rain	5	1.86	0.07	-449.02
stage + plot + high temperature	4	1.97	0.06	-450.08
stage + plot + day of year	4	1.99	0.06	-450.09
stage*plot + camera	5	2.66	0.04	-449.42
stage*plot +interval rain	5	2.89	0.04	-449.54
stage*plot + high temperature	5	3.25	0.03	-449.71
stage*plot + day of year	5	3.28	0.03	-449.73
plot	2	3.65	0.03	-452.93
plot + daily rain	3	3.70	0.03	-451.95
plot + camera	3	4.50	0.02	-452.35
stage + plot + year	6	5.27	0.01	-449.72
plot + interval rain	3	5.31	0.01	-452.75
plot + yearday	3	5.43	0.01	-452.81
plot + high temperature	3	5.55	0.01	-452.87
stage*plot + year	7	6.58	0.01	-449.36

K = number of model parameters, $\Delta AIC_c = AIC_c$ distance from top-ranked model, w_i = Akaike weight, LL = log-likelihood

[1]Top-ranked model $AIC_c = 906.21$

[2]Models with $w_i < 0.01$ not shown

Table A1.4. Parameter estimates from models ranked within 4 AICc units of the top-ranked model of daily survival rate in Australia.

Fixed effect	Estimate[1]	SE	85% CI	95% CI
camera	-0.23	0.2	{-0.51, 0.06}	{-0.61, 0.16}
daily rain	0.05	0.04	{-0.01, 0.11}	{-0.03, 0.13}
interval rain	-0.14	0.14	{-0.06, 0.33}	{-0.13, 0.41}
high temperature	0.01	0.04	{-0.04, 0.07}	{-0.06, 0.09}
day of year	-0.001	0.003	{-0.006, 0.004}	{-0.008, 0.006}
age^2	-3.01	4.46	{-9.30, 3.49}	{-11.52, 5.91}

[1]All parameter estimates are from models also including the fixed effect age*year, except for age^2, which is from a model including fixed effects of age and year.

Table A1.5. Parameter estimates from models ranked within 4 AICc units of the top-ranked model of daily survival rate on Rota.

Fixed effect	Estimate[1]	SE	85% CI	95% CI
daily rain	-0.03	0.02	{-0.06, 0.007}	{-0.08, 0.22}
camera	0.19	0.26	{-0.17, 0.57}	{-0.30, 0.72}
interval rain	0.12	0.2	{-0.16, 0.41}	{-0.27, 0.51}
high temperature	0.02	0.09	{-0.12, 0.15}	{-0.17, 0.20}
day of year	0.0003	0.003	{-0.004, 0.005}	{-0.005, 0.006}
stage*plot	0.39	0.46	{-0.26, 1.07}	{-0.49, 1.33}

[1]All parameter estimates are from models also including the fixed effects of stage and plot.

Chapter 2: Relaxed nestling-stage predation risk and the life history syndrome of an insular Rufous Fantail subspecies

INTRODUCTION

Nest predation is an important source of selection on avian parental care and offspring development strategies (Martin and Briskie 2009). Among passerine and near-passerine birds, offspring of species that are more susceptible to nest predation fledge at earlier ages (Martin 1995, Roff et al. 2005) and develop locomotor traits more rapidly (Ferretti et al. 2005, Cheng and Martin 2012), despite being fed at lower rates (Martin et al. 2011, Martin 2015). The evolution of faster development despite less frequent provisioning suggests that offspring are under selection to prioritize resources for growth when faced with high predation risk (Remes and Martin 2002, Dmitriew 2011, Cheng and Martin 2012). Although many species reduce provisioning rates in response to acute predation risk (Skutch 1949, Peluc et al. 2008), such plasticity following introduction of non-native predators (e.g. Massaro et al., 2008) may not buffer native birds against the effects of invasive predators if growth strategies are not equally labile.

Due to the absence of native mammalian and reptilian predators, oceanic island bird species are expected to have relatively 'slow' (i.e. more K-selected) life history syndromes in which high nest success and adult survival are reflected in increased parental investment per offspring and reduced offspring growth rates relative to continental species (Covas 2012). Previous comparative literature reviews documented longer nestling development periods and larger egg size on islands than on continents (Grant and Grant 1980, Trevelyan and Read 1989, Bosque and Bosque 1995, Covas

2012). Despite conservation concerns about the impact of non-native predators on island birds (e.g. Savidge 1987, Thibault et al. 2002, Blackburn et al. 2004), detailed *in situ* studies of related island and continental taxa are lacking. For example, longer development periods and/or increased provisioning rates could increase the probability that a predator will discover a nest and thus may explain some of the vulnerability of island birds to non-native predators. While the length of the nestling period is inversely correlated with offspring growth rates across species (Martin et al. 2011, Martin 2015), understanding specifically which traits experience differences in selection between continental and island birds warrants further study. Additionally, understanding how behavioral assays of parental investment (provisioning and nest guarding) co-vary with growth rate will help determine the extent to which nestling development periods on islands are driven by food limitation (Ashmole 1963) or relaxation of predation risk (e.g. Martin et al. 2011).

Rufous Fantails (*Rhipidura rufifrons*, hereafter 'fantails') are widely distributed throughout islands and continental land masses in western Oceania (Dickinson 2003). In Chapter 1, I showed that island fantails experienced higher nest predation rates during incubation than during the nestling period. By contrast, nest predation rates increased significantly in the final days of the nestling period for continental fantails, largely due to predation by reptiles (Chapter 1). This interaction between age-dependent predation risk and site is consistent with the presence of strong selection at my continental site to minimize nestling-stage predation risk by earlier fledging. Since aerial foragers like fantails are thought to be more affected by food availability than other passerines (Murphy 1983, Martin 1995, Remes and Martin 2002) brood

size is an important factor to consider in my study. In this study, I 1) compare life history traits between island and continental fantail subspecies and 2) examine variation in life history traits as a function of brood size within each site. I predict that during the nestling stage, island fantails will have higher parental investment (per-nestling provisioning and nest guarding rates) but slower growth of locomotor traits, due to the lower nestling-stage nest predation rate I observed at my island site (Chapter 1).

METHODS

Study system

Fantails are forest-dependent flycatchers (8-10 g) that build shrub or sub-canopy cup nests, which are attended by both sexes during the incubation and nestling periods. I studied fantails from September – January (2014 – 2016) in Iluka Nature Reserve, New South Wales, Australia (*rufifrons* subspecies; 29°24'19" S, 153°21'34" E; hereafter 'Australia') and from March – June (2013 – 2015 and 2017) on Rota, Commonwealth of the Northern Mariana Islands (*mariae* subspecies; hereafter 'Rota') at two different study plots on public land (14.1776°N, 145.2067°E and 14.1554°N, 145.2499°E) Fantails have multiple broods per season at both sites; however, they are migratory, seasonal breeders at my Australian site, while breeding nearly year-round on Rota. See Chapter 1 for a detailed description of study sites.

Data collection

To compare fantail clutch size, egg size, developmental periods and rates of parental provisioning, nest guarding, and nestling growth between study sites, I located and monitored nests as described in Chapter 1. I checked nest contents every 2 – 4 days, with

checks occurring daily or twice daily around hatching and fledging to accurately measure incubation and nestling period lengths. If the nest was found empty prior to two days before the modal fledgling age (11-12 days in Australia and 13 days on Rota), I assumed the nest had failed. Video recording for a separate study on nest predation (Chapter 1) corroborated these assumptions—nestlings did not successfully fledge before 10 days in Australia and 11 (usually 12 or 13) days on Rota (L. Nietmann, unpublished data). If the nest was found empty within two days of the expected fledging age I searched the area for fledglings. If the adults were located without fledglings and/or were found building a new nest on the same territory, I assumed the nest had failed. Adults were identified by color-bands (Chapter 4) and/or territory occupancy. I recorded clutch size only for nests found prior to clutch completion, since partial predation could bias estimates of clutch size (L. Nietmann, unpublished data). I also excluded nests that were too high (> 6 m) to discern clutch size with the aid of a mirror pole. I measured egg size (length and width) using digital calipers (precision = 0.01 mm) and mass using a digital scale (precision = 0.001 g) within three days of clutch completion to minimize change in mass due to water loss (Rahn and Ar 1974). Egg volume was calculated following Hoyt (1979).

I used DCR-SX85 video-recorders (Sony, Tokyo, Japan) to measure nestling provisioning rates at each site on the day the nestlings' wing pin feathers broke their sheaths (generally 8 days after hatching, hereafter 'pin break day'). Restricting video-recording to pin break day allowed developmental stage to be controlled between broods. I placed unattended cameras 5-10 m from nests and excluded the first 10 min of recording from analysis to reduce any effects of human presence on provisioning behavior. Video-recording commenced within 30 min after sunrise and continued for 4-5

hours. I later coded videos to measure the number of feeding trips to the nest per nestling per hour ('per nestling provisioning rate') as a proxy for parental investment (Martin 2015). I also estimated the size of each prey item relative to the fantails' bill size (i.e. 'food loading'), because prey item size could compensate for a reduction in per-nestling feeding rate. I categorized food loading using the following rating scale: 1 = prey item contained entirely inside the adult's bill (i.e. not visible), 2 = prey item visible between mandibles but gap between mandibles less than the depth of the bill at its base and 3 = prey item visible between mandibles and gap between mandibles greater than the depth of the bill at its base. Occasionally it was not possible to estimate food loading due vegetation obstructing the adult's bill and/or the angle of the camera relative to the feeding event. Therefore, instead of calculating total food delivery per hour (Martin 2000), I present food loading data in terms of the average prey item size for each nest.

Nest guarding observations were also conducted on pin break day, beginning 1-3 hours after sunrise. At least 24 hours before the observation, I delineated a circular plot (113 m^2) centered on the nest by placing flagging tape 6 m from the nest in each of the four cardinal directions. I chose to monitor plots of this size based on preliminary observations of nest guarding behavior: fantails generally perch within 6 m of the nest and forage outside this area. There were clear sight lines within this range at both study sites. On the morning of observation, an observer concealed in a camouflaged blind 7-10 m from the nest used a portable voice recorder to note when each fantail entered and exited the plot, as well as their behavior while inside this focal area. Observations lasted 50 min, after an initial 10 min habituation period. I quantified nest guarding: 1) as the sum of the time each adult fantail spent within the observation plot during which they

were not engaged in feeding or brooding nestlings ('total nest guarding time') and 2) as the total time divided by the number of times an individual fantail entered the plot ('nest guarding time per visit'). Generally, fantails guarded their nests immediately after feeding their nestlings. Therefore, reporting nest guarding time per visit controlled for potential confounding with provisioning rate.

To compare nestling growth rates, I measured nestlings every other day starting on hatch day or the day after hatch until the last day I could approach a nest without force-fledging (10 and 11 days after hatching in Australia and Rota, respectively). I measured nestling mass with a digital scale (precision = 0.01 g), tarsus length with digital calipers (precision = 0.01 mm), and flattened wing length from the carpal joint to the tip of the longest flight feather (or sheath) to the nearest 0.5 mm using a ruler with a wing stop. I measured all nestlings between 1200 and 1800 h and made measurements for each nest at a similar time of day (± 45 min). Prior to analysis, I scaled nestling measurements to the average adult measurement of each trait at each site to account for morphometric differences of adults between my study populations (Chapter 4).

Data analysis

I analyzed data using R 3.4.2 (R Core Team 2017) and evaluated results using the information-theoretic paradigm (Burnham et al. 2011). I assessed differences in clutch size, egg mass, egg volume, and incubation and nestling period lengths by determining whether the 95% confidence interval of the effect size (Hedge's d) overlapped zero (Nakagawa and Cuthill 2007). To compare differences in per nestling provisioning rate between sites and between brood sizes, I constructed a candidate set of four general linear models (GLMs) including fixed effects of site, brood size, additive effects of site and

brood size, and a site by brood size interaction (Table A2.1). Next, I used GLMs to examine whether variation in food loading was better explained by site or by per-nestling feeding rate. I then modelled total nest guarding time with a candidate set of four GLMs containing these same fixed effects (Table A2.1). Finally, I examined a potential tradeoff between guarding the nest and provisioning offspring using a separate set of GLMs with nest guarding time per visit as the dependent variable. Candidate models included fixed effects of site, brood size, provisioning rate, additive effects of these variables, and a provisioning rate by site interaction (Table A2.1). I ranked candidate models by Akaike's Information Criterion corrected for small sample size (AIC_c) and determined parameter estimates by averaging over all models ranked within 4 AIC_c units of the top-ranked model (Mazerolle 2017).

I calculated nestling growth rates by fitting nonlinear models (Pinheiro et al. 2017) of mass, wing length and tarsus length using the logistic growth equation: $W(t) = A/[1 + e^{-K(t-t_i)}]$, where W(t) is the measurement at time t, A is the asymptotic measurement value nestlings approach, t_i is the inflection point of the growth curve on the time axis and K is a standardized measurement of peak growth rate that is commonly used in comparative studies (Ricklefs 1968, Remes and Martin 2002). Prior to fitting models for growth rate of mass, I truncated measurements at the maximum mass attained for one 1 of the 25 nestlings measured on day 8 or older in Australia to avoid downward bias due to mass regression (Remes and Martin 2002). None of the 32 nestlings measured on day 8 or older on Rota experienced mass regression. I fit separate logistic growth models for each brood size (1 or 2 nestlings) as well as for all broods combined at each site. I compared differences in growth rate between sites and between brood sizes within

each site by simulating each K estimate from a multivariate normal distribution (N = 10000, R function *mvrnorm*). I then determined whether the magnitude of the difference between pairs of simulated K values was greater than zero by calculating the mean difference and associated 95% confidence intervals for each comparison. I also calculated the average growth rate (K_{avg}) by averaging the derivative of the growth curve (scaled to K by multiplying by 4/A) for nestlings at 1000 points spaced equally over the entire measurement period, following Martin (2015).

RESULTS

Clutch size did not differ between sites (range: 1- 2 eggs, Table 2.1). I observed one brood of three nestlings in Australia, but this nest was found after hatching and thus did not meet my inclusion criteria for the clutch size calculations. Fantail eggs in Australia were 7% larger and 7% heavier than eggs on Rota, but after controlling for average female mass there was no difference in egg volume or mass between sites (Table 2.1). The length of the incubation period did not differ between sites, but the nestling period was 10% longer on Rota (Table 2.1).

Parental investment, as measured by per-nestling provisioning rate, was 46.3% higher on Rota (14.72 ± 0.59 trips hr^{-1}) than in Australia (10.06 ± 0.55 trips hr^{-1}; Table 2.2). Per-nestling provisioning rates did not differ between brood sizes at either site (Table 2.2). On average, fantails delivered larger prey items to nestlings in Australia (1.94 ± 0.06) than on Rota (1.75 ± 0.04; d = 0.92, 95% CI: 0.26, 1.57; Fig. 2.1A). However, after accounting for the inverse relationship between food load size and per-nestling provisioning rate, site was not an important predictor of prey item size (Table 2.2, Fig. 2.1B).

Fantails spent 137% more total time guarding their nests per 50 min observation period on Rota (39.55 ± 1.84 min) than in Australia (16.64 ± 1.11 min). Nest guarding time per visit was 63% higher on Rota (1.99 ± 0.16 min) than in Australia (1.22 ± 0.11 min), but at both sites nest guarding time per visit declined with provisioning rate (Fig. 2.2). There was not an effect of brood size on total nest guarding time or nest guarding time per visit (Table 2.2).

Nestlings in Australia had 11% faster peak wing growth rates and 13% faster peak tarsus growth rates than on Rota (Fig. 2.3, Table 2.3). Nestling wing and tarsus growth rates also peaked earlier in Australia (wing: 5.4 d, tarsus: 2.9 d) than on Rota (wing: 6.2 d, tarsus: 3.9 d; Fig. 2.3, Table 2.3). There was no difference in mass growth rates between Rota and Australia, and nestlings at both sites experienced peak mass growth on the fourth day after hatching (Fig. 2.3, Table 2.3). Nestlings on Rota had a slower post-peak deceleration of wing and tarsus growth than nestlings in Australia, but post-peak mass growth rate was similar between sites (Fig. 2.3). There was no effect of brood size on peak growth rate of wing, tarsus or mass at either site (Table 2.3).

DISCUSSION

Fantails on Rota had slower peak growth rates of nestling locomotor traits, higher rates of provisioning and a longer nestling development period than fantails in Australia. This life history syndrome was expected because fantails on Rota experience relaxation of nestling-stage nest predation relative to Australia (Chapter 1) and previous research suggests that nest predation selects for faster nestling development and parental provisioning rates (Ferretti et al. 2005, Cheng and Martin 2012, Martin 2015). I did not find evidence that food availability influenced life history variation because 1) life history

traits did not vary between brood sizes at either site and 2) nestling growth rates were higher in Australia, where nestlings were fed less often.

I found that nestlings' wings and tarsi attained peak growth at earlier ages and reached higher maxima in Australia than on Rota, but there was not a difference in mass growth rate between sites. This suggests that fantails in Australia partition resources toward rapid growth of locomotor traits, whereas fantails on Rota have a growth strategy that favors the development of other internal systems, perhaps to increase post-fledging and/or adult survival (e.g. Martin 2015). Rapid growth is thought to be physiologically costly (Dmitriew 2011), thus it may be expected to evolve only in environments where it is under strong selection. Predation risk increases significantly with nestling age in Australia (Chapter 1), applying selective pressure on locomotor growth to allow earlier fledging (Remes and Martin 2002). For example, in Australia juvenile fantails survived to independence from their parents after force-fledging 10 days after hatching, whereas on Rota 10-day old nestlings did not attempt to escape when a predator approached the nest. Even 11-day old nestlings on Rota were generally preyed upon instead of force-fledging, which is interesting because 11-day old nestlings fledged naturally (i.e., not forced by a predator) in Australia (L. Nietmann, personal observation).

Nestlings in Australia grew more rapidly despite being fed less often than nestlings on Rota, likely because higher nestling-stage nest predation favors both faster growth and lower provisioning rates (Ferretti et al. 2005, Martin et al. 2011). Lower provisioning in Australia could be caused by decreased investment in current reproduction, due to the higher probability of nestling-stage predation (Chapter 1) and the need to save energy for future nest attempts (Martin 2014). The elevated risk of nestling

predation in Australia could also favor a reduction in nest attendance to avoid attracting visually oriented predators to the nest (Skutch 1949, Martin et al. 2000). Fantails appear to compensate for reduced feeding rates by carrying more food per trip (Fig. 2.1B), providing support for the hypothesis that low feeding rates in Australia function to reduce visual cues to nest location (Martin 2000, Muchai and du Plessis 2005). Site-specific differences in food loading (Fig. 2.1A) were explained entirely by feeding rate, indicating that food loading arises from plasticity rather than heritable behavioral differences or variation in the size of available prey items between sites.

Previous work suggests that nest guarding rate is positively related to both nest predation risk and food availability (Martin 1992, Komdeur and Kats 1999, Rastogi et al. 2006). However, I found that fantails spent more time guarding their nests on Rota than in Australia, despite the fact that nestling-stage predation rate was higher in Australia (Chapter 1). I also found evidence of a tradeoff between nest guarding and provisioning at both sites (Fig. 2.2). Fantails in Australia may spend less time guarding their nests due to reduced parental investment and/or the need to spend more time foraging for themselves in order to maintain energy reserves for future reproduction (Martin 1992). Alternatively, the benefit of nest guarding might be higher on Rota than in Australia due to differences in nest predator community composition. Fantails on Rota can deter the predominant nest predators (passerine and near-passerine birds), whereas fantails are ineffective at defending against lace monitors (*Varanus varius*; personal observation), the principal nest predator in Australia (Chapter 1). Therefore, fantails—and possibly passerine birds in general—may follow different strategies for maximizing reproductive success that depend on predator community composition. In Australia, nestlings grow

faster and fledge earlier, since the risk of predation increases with nestling age (Chapter 1) and parents cannot deter common nestling-stage predators (personal observation). By contrast, nestlings on Rota have slower, more sustained growth, since nestling-stage predation risk is relatively low and parents can deter the predominant nest predators by guarding the nest (personal observation).

I acknowledge that my results are potentially confounded by other factors that could explain differences in parental investment and nestling growth strategies between my study sites. For example, the Australian population is migratory and thus has a shorter breeding season, which could favor accelerated offspring development (Young 1996). However, the lower nestling provisioning rates in Australia are better explained by nest predation (e.g. Ferretti et al. 2005, Martin et al. 2011) than by breeding season length, since it is unclear why a shorter breeding season would favor lower rates of food delivery. Adult mortality is another alternative explanation, since native predators of adult Fantails do not occur on Rota and this lower mortality risk is expected to cause a slower life history syndrome (Gill and Haggerty 2012, Martin 2015, Boyce and Martin 2017). Unfortunately, I was unable to measure adult survival at my study sites due to concerns that injuries caused by color bands had biased survival rates (Chapter 4). Ultimately, although other factors may contribute to life history variation between my study sites, differences in nestling-stage predation risk (Chapter 1) offer a parsimonious explanation for my results.

Relaxed selection on islands may explain some of the vulnerability of insular birds to non-native predators. Longer nestling periods expose offspring to elevated time-dependent nest mortality, which may be problematic if introduced predators locate nests

using cues that increase in the final days of the nestling stage (e.g. Stake et al. 2005, Chapter 1). Additionally, higher nestling provisioning rates may increase predation by visually oriented predators (Martin et al. 2000, Muchai and du Plessis 2005; but see Pope et al. 2013). Thus, the slower life history syndrome of island birds may explain some of their vulnerability to non-native predators. Island birds are able to adaptively adjust nestling provisioning rates in the face of a novel predation risk (Massaro et al. 2008, Peluc et al. 2008). However, future studies should also examine the plasticity of insular nestlings' growth strategies, given evidence that pre-ovulatory exposure to predation risk can increase post-natal growth rates in a continental passerine (Coslovsky and Richner 2011). If island nestlings have limited plasticity, eradication of non-native predators is likely a better management strategy than anti-predator training (e.g. Maloney and McLean 1995). Thus, future studies should consider plasticity of life history traits among insular species in order to inform conservation strategies

FIGURES

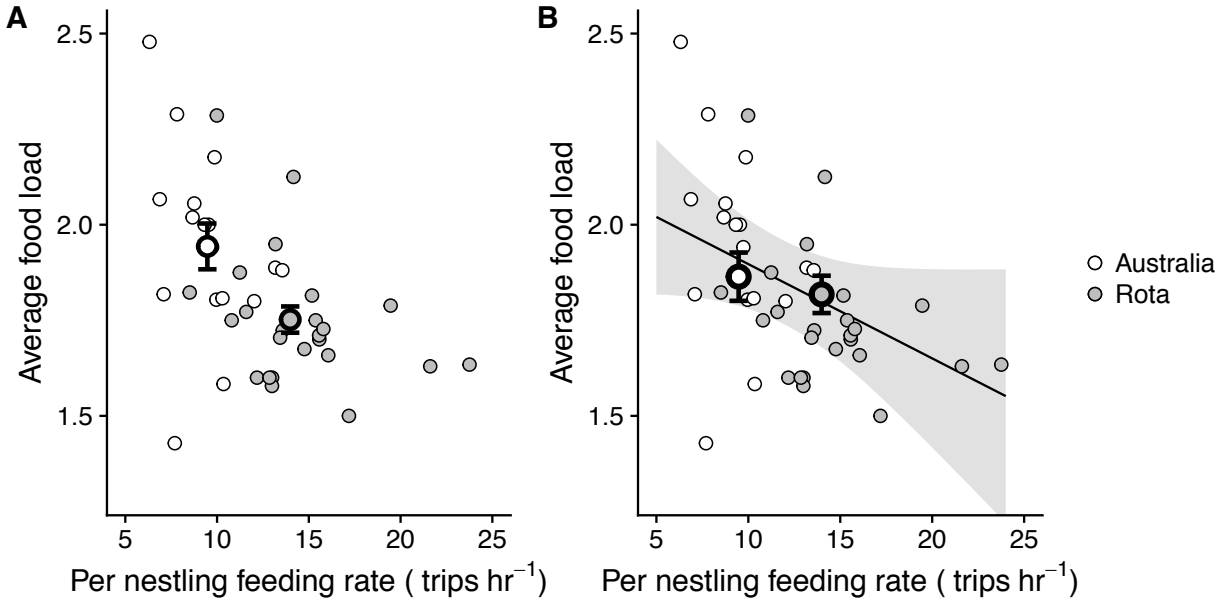

Figure 2.1. Average food load size and per nestling feeding rate are inversely related when data is pooled across sites. Although on average, Rufous Fantails fed larger prey items to nestlings in Australia (A), after accounting for variation in food load size explained by feeding rate, there was no difference between sites (B). Error bars show ± SE around average food load size (A) and model predictions of food load size in (B).

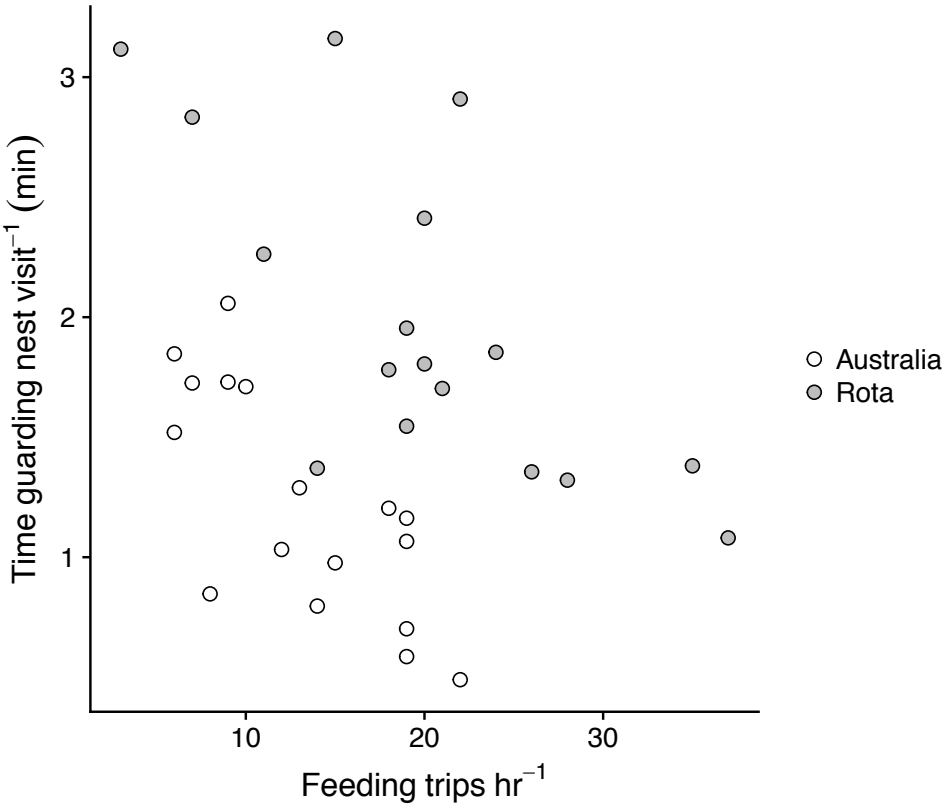

Figure 2.2. The time Rufous Fantails spent guarding their nests per visit declined with provisioning rate, suggesting a tradeoff between these two activities. On average, Rufous Fantails spent more time guarding their nests per visit on Rota than in Australia.

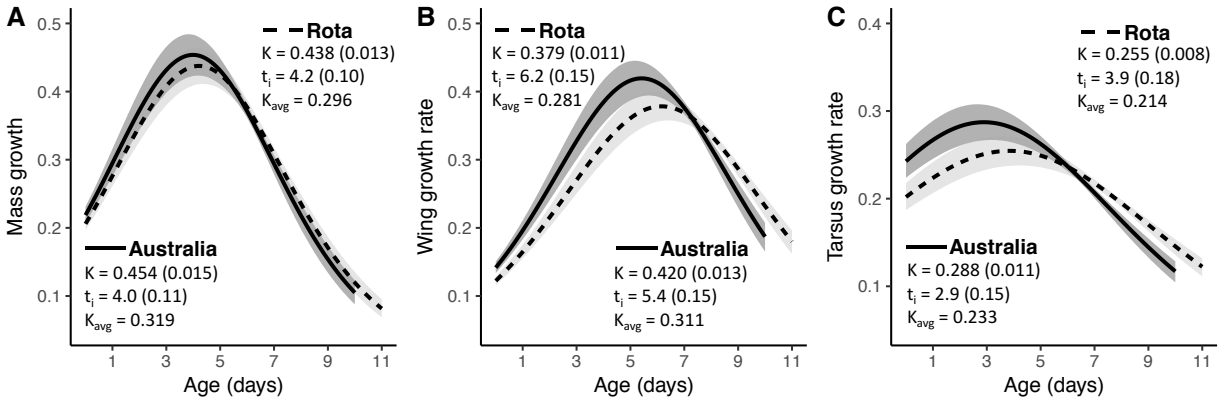

Figure 2.3. Instantaneous growth rates of mass (A), wing length (B) and tarsus length (C) from hatching (age = 0) to one day prior to fledging for Rufous Fantail nestlings in Australia and Rota. Growth rate of mass followed a similar trajectory between sites, but nestlings in Australia grew wings and tarsi faster early in the nestling period and reached higher peak growth than nestlings on Rota, which maintained a higher growth rate after reaching peak growth. Peak growth (K ± SE) and age at peak growth (t_i ± SE) as well as instantaneous growth rate averaged over the entire time period (K_{avg}) are indicated for each site. Shaded areas show 95% CIs (drawn from multivariate normal simulation) for each curve.

TABLES

Table 2.1. Rufous Fantail life history traits in Australia and Rota (mean ± SE).

	Australia	Rota	Effect size[1]	95% CI[2]
Clutch size	1.98 ± 0.01 N = 187	1.98 ± 0.01 N = 174	0.01	{-0.20, 0.22}
Egg volume (mL)	1.50 ± 0.02 N = 42	1.40 ± 0.02 N = 34	0.71	**{0.25, 1.18}**
Standardized Volume	0.17 ± 0.002 N = 42	0.17 ± 0.002 N = 34	-0.04	{-0.49, 0.41}
Egg mass (g)	1.56 ± 0.02 N = 42	1.46 ± 0.01 N = 34	1.06	**{0.57, 1.54}**
Standardized Mass	0.17 ± 0.002 N = 42	0.17 ± 0.001 N = 34	0.06	{-0.40, 0.51}
Incubation period	15.16 ± 0.05 N = 55	15.08 ± 0.04 N = 49	0.25	{-0.14, 0.63}
Nestling period	11.57 ± 0.16 N = 30	12.71 ± 0.12 N = 28	-1.43	**{-2.01, -0.85}**

[1]Hedge's d

[2]Bold values indicate 95% CIs around effect sizes that do not overlap zero.

Table 2.2. Relationships between predictor variables and per-nestling provisioning rate, total time guarding nest and nest guarding time per visit.

Model set	Parameter[1]	Estimate[2]	95% CI[3]
Per nestling provisioning rate (N = 58)	Site	4.86	**{2.84, 6.88}**
	Brood size	0.55	{-1.83, 2.93
	Site x Brood size	-2.21	{-5.51, 1.09}
Food loading (N = 41)	Site	-0.11	{-0.29, 0.07}
	Per-nestling feeding rate	-0.03	**{-0.05, -0.01}**
Total time guarding nest (N = 36)	Site	22.91	**{18.67, 27.14}**
	Brood size	1.08	**{-3.39, 5.54}**
Nest guarding time per visit (N = 36)	Site	1.11	{**0.66, 1.57**}
	Feeding rate	-0.06	**{-0.09, -0.03}**
	Feeding rate x Site	0.01	**{**-0.03, 0.06**}**
	Brood size	-0.09	{-0.53, 0.35}

[1]Reference levels are Australia (for 'site') and one-nestling broods (for 'brood size')

[2]Estimates and CIs are model-averaged [3]Bold values indicate that the CI does not overlap zero.

Table 2.3. Difference in nestling wing, tarsus and mass growth rates by site and by brood size within each site.

Measurement	Comparison	N[1]	Difference[2]	95% CI[3]
Wing	Site	102	0.041	**{0.008, 0.074}**
	Brood size (Australia)	55	0.021	{-0.047, 0.089}
	Brood size (Rota)	47	0.006	{-0.036, 0.047}
Tars	Site	102	0.033	**{0.007, 0.059}**
	Brood size (Australia)	55	0.014	{-0.036, 0.064}
	Brood size (Rota)	47	-0.008	{-0.039, 0.023}
Mass	Site	102	0.016	{-0.025, 0.056}
	Brood size (Australia)	55	0.016	{-0.048, 0.081}
	Brood size (Rota)	47	0.007	{-0.045, 0.059}

[1]Number of nestlings [2]Positive values indicate faster peak growth in Australia (for 'site') and in one-nestling broods (for 'brood size') [3]Bold values highlight 95% CIs that do not overlap zero.

APPENDIX

Table A2.1. Summary of models in each candidate set (i.e. for each dependent variable), ranked by AIC_c.

Candidate set	Parameters[1]	K	AIC_c	ΔAIC_c	AIC_c weight	Cum. weight	Log Likelihood
Per nestling provisioning rate	S	3	293.50	0.00	0.65	0.65	-143.53
	S + B	4	295.82	2.32	0.20	0.85	-143.52
	S*B	5	296.41	2.91	0.15	1.00	-142.62
	Intercept	2	317.62	24.12	0.00	1.00	-156.70
	B	3	319.79	26.28	0.00	1.00	-156.67
Food loading	P	3	-11.70	0.00	0.61	0.61	9.17
	S + P	4	-10.24	1.46	0.29	0.29	9.67
	S	3	-8.02	3.68	0.10	1.00	7.33
	Intercept	2	-2.06	9.63	0.00	1.00	3.19
Total time nest guarding	S	3	226.12	0.00	0.72	0.72	-109.66
	S + B	4	228.46	2.34	0.22	0.94	-109.54
	S*B	5	231.09	4.97	0.06	1.00	-109.47
	Intercept	2	275.14	49.02	0.00	1.00	-135.38
	B	3	277.50	51.38	0.00	1.00	-135.35
Nest guarding time per visit	F + S	4	42.93	0.00	0.61	0.61	-16.78
	F*S	5	45.36	2.43	0.18	0.79	-16.61
	F + S + B	5	45.52	2.59	0.17	0.96	-16.69
	F*S + B	6	48.27	5.34	0.04	1.00	-16.58
	S + B	4	54.11	11.18	0.00	1.00	-22.36
	S	3	64.45	21.51	0.00	1.00	-28.82
	B	3	69.18	26.25	0.00	1.00	-31.19
	F + B	4	71.73	28.80	0.00	1.00	-31.17
	F	3	74.45	31.52	0.00	1.00	-33.83
	Intercept	2	75.03	32.10	0.00	1.00	-35.32

[1]S = Site, B = Brood size, P = Per-nestling provisioning rate, F = Number of feedings per 50 min observation period

Chapter 3: Nest site characteristics and nest reuse in island and continental Rufous Fantails

INTRODUCTION

Eggs and altricial offspring of passerine birds are vulnerable to predation while in the nest (DeGregorio et al. 2016), prompting studies of the adaptive value of nest site selection. Nest sites are often distinguishable from the surrounding habitat (Chase 2002, Rangel-Salazar et al. 2008, Ha et al. 2011) and successful nest sites differ from those discovered by predators (Martin and Roper 1988, Hatchwell et al. 1999, Liebezeit and George 2002, Koenig et al. 2007, Colombelli-Négrel and Kleindorfer 2009). However, some studies do not detect a relationship between nest site characteristics and nest success (Filliater et al. 1994, Sachtleben 2005), either because nest site characteristics are already at an adaptive peak (Latif et al. 2012), different predator species locate nests using distinct foraging modalities (Remeš 2005, Benson et al. 2010), or latent, unmeasured nest site characteristics influence nest survival (Chalfoun and Schmidt 2012).

Concurrently studying nest site characteristics and nest reuse allows the assessment of whether latent nest site characteristics influence nest survival by comparing nest fates across repeated attempts at the same nest site. Nest site safety is one possible explanation for some species' reuse of successful nest sites for subsequent breeding attempts within and between breeding seasons (Blancher and Robertson 1985, Ellison 2008). However, in some avian species nest reuse does not appear to increase the probability of nest survival. For example, in Eastern Kingbird (*Tyranus tyranus*) and

Marsh Tit (*Poecile palustris*), nest site reuse does not result in higher nest survival when compared to building a new nest (Wesołowski 2006, Redmond et al. 2007). Similarily, in Spotted Antbirds (*Hylophylax naevioides*), nest fate is not repeatable across subsequent attempts at the same nest site (Styrsky 2005). This indicates that for some species, nest predation is unpredictable and may be driven more by predator spatial behavior than by nest site characteristics (Vickery et al. 1992).

I compared nest site characteristics and subsequently described patterns of nest reuse in two Rufous Fantail (hereafter 'fantail') sub-species: *Rhipidura rufifrons rufifrons* in Iluka, New South Wales, Australia (hereafter 'Australia') and *R. r. mariae* on the island of Rota, Commonwealth of the Northern Mariana Islands, USA (hereafter 'Rota'). Oceanic islands like Rota generally have a reduced diversity of native carnivorous reptiles and small mammals. The introduction of these predators has caused the decline or extinction of many forest birds (Savidge 1987, Blackburn et al. 2004). Fantails (*R. r. uraniae*) and all other native cup-nesting forest birds were rapidly extirpated from the island of Guam (60 km from Rota) following the introduction of the brown treesnake (*Boiga irregularis*; Savidge 1987). The slower decline of several non-native cup-nesting species and one native cavity-nesting species on Guam (Wiles et al. 2003) suggests a role of nest site safety in species' vulnerability to brown treesnake predation (cavity nests generally experience lower predation rates than cup nests, Martin 1995). Indeed, the persistence of fantails and other forest birds in the brown treesnake's native range (Australia, Solomon Islands, Papua New Guinea) suggests that birds on Guam may be uniquely susceptible to snake predation. Bird taxa that have historically experienced nest

predation by reptiles and mammals may have evolved a nest site selection strategy that minimizes predation risk from these predators.

Using Rota as a proxy for Guam, I expect nest site characteristics that restrict access to reptilian predators (e.g. lower vegetation connectivity and higher placement above ground: Burhans et al. 2002, Koenig et al. 2007, Chiavacci et al. 2014, DeGregorio et al. 2016) or that increase the opportunity birds have to detect reptilian predators (e.g. smaller branch diameter, longer branch length) to be greater in Australia than on Rota. Additionally, I expect that these characteristics will predict nest success in Australia, where climbing predators are common and on Rota, where non-native rats are occasional nest predators (Chapter 1). Finally, I predict that nests that are reused following fledging will have a higher probability of survival than newly built nests at both study sites due to intrinsically higher nest site quality.

METHODS

Study system

Fantails are small (8-10 g) forest flycatchers distributed throughout western Oceania. I studied fantails from September – January (2014 – 2016) in Australia (29°24’19” S, 153°21’34” E) and from March – June (2013 – 2015 and 2017) on Rota at two different study plots on public land (14°10’43” N, 145°12’30” E and 14°9’18” N, 145°14’54” E). Fantails have multiple broods per season at both sites. However, they are migratory, seasonal breeders at my Australian site, while breeding nearly year-round on Rota (Higgins et al. 2006, Pyle et al. 2008). Fantails build cup nests in shrubs and sub-canopy trees using spider webs, dead plant material and rootlets. Both sexes participate in nest

site selection, but the female does the majority of nest construction (L. Nietmann, personal observation).

At my Australian site, lace monitor lizards (*Varanus varius*) are common nest predators, while Laughing Kookaburras (*Dacelo novaeguineae*), hawks (*Accipiter* spp.) and a variety of passerine birds also consume eggs and nestlings (Chapter 1). On Rota, Mariana Crows (*Corvus kubaryi*) are the principal nest predator species. The only other native nest predators are passerine and near-passerine birds (Chapter 1). Non-native rats (*Rattus diardii* sensu Wiewel et al. 2009) and Black Drongos (*Dicrurus macrocercus*) also prey upon nests (Baker 1951, Steadman 1999, Chapter 1). Mangrove monitor lizards (*Varanus indicus*) occur on Rota, although the origin of the population is debated (Steadman 1999, Cota 2008, Pregill and Steadman 2009) and monitor lizards do not appear to be important nest predators (Chapter 1).

Data Collection

I located and monitored nests as described in Chapter 1. I checked nest contents every 2 – 4 days, with checks occurring daily or twice daily around hatching and fledging. If the nest was found empty prior to two days before the modal fledgling age (11 days in Australia and 13 days on Rota), I assumed the nest had failed. Video recording for a separate study on nest predation (Chapter 1) corroborated these assumptions—nestlings did not successfully fledge before they were 10 days old in Australia and 11 (usually 12 or 13) days old on Rota (L. Nietmann, unpublished data). If the nest was found empty within two days of the expected fledging age, I searched the area for fledglings. If the adults were located without fledglings and/or were found building a new nest on the same territory, I assumed the nest had failed. Adults were identified by color-bands (Chapter 4)

and/or territory occupancy. Nest predation is the most common cause of nest failure in my study system (Chapter 1) therefore unless there was evidence of failure caused by weather or nestling starvation, I assumed nests failed due to predation.

I measured nest site characteristics for 241 of 314 nests found in Australia and 179 of 307 nests found on Rota. All measurements were recorded within two weeks of nest failure or fledging. Nests that failed due to hatching failure were generally reused immediately after the parents removed the eggs (L. Nietmann, unpublished data). Therefore, in order to avoid causing nest abandonment, I did not record measurements following hatching failure and instead measured nest site characteristics after the second nest attempt at the nest site had fledged or failed. However, for all nest site analyses, I used only the first nest attempt at each nest site in subsequent analyses to ensure that observations were independent. At each nest site, I characterized the placement of the nest cup by measuring the height of the cup rim above ground ('height'), the shortest distance between the nest cup and the trunk of the tree ('distance'), the distance between the nest cup and trunk of the nest tree along the branch supporting the nest ('branch distance'), the total length of the branch supporting the nest ('branch length'), the diameter of the trunk of the tree containing the nest at 1 m above ground ('trunk diameter'), the diameter of the branch supporting the nest cup at the nest site ('support diameter') and the diameter of the branch supporting the nest cup 10 cm from the trunk of the tree ('branch diameter'). I also identified the species of tree or shrub supporting the nest, counted the number of other branches that crossed the branch supporting the nest ('paths') and counted the number of branchlets supporting the nest cup ('branchlets'). For nest sites that I could access on foot or with a ladder (< 3.8 m above ground), I measured

all of these characteristics. For nests greater than 3.8 m above ground, I only recorded height (using a telescoping pole), distance (estimated by measuring distance on the ground from directly below the nest cup to the trunk), trunk diameter and plant species. Of the nests measured, 68 (28%) and 123 (69%) received the complete battery of measurements in Australia and Rota, respectively.

I defined nest reuse as a clutch initiated in a nest that had been constructed and then used in a previous breeding attempt during the same breeding season. Observations of color banded birds and detailed territory maps indicated reuse of nests by the same breeding pair that built the initial nest. It is possible that I underestimated the rate of nest reuse at each site since nests found after clutch initiation could have been reused from a previous attempt (i.e. the data are left censored). I categorized nests found when they were less than 50% complete as 'newly built' to compare the potential nest survival advantage of reusing an old nest versus building a new nest.

Data Analysis

I used R version 3.4.2 to perform all statistical analyses (R Core Team 2017). I performed Principal Component Analysis (PCA) on a correlation matrix to reduce the numeric nest site measurements into orthogonal principal components. Since I was able to measure the complete battery of nest site characteristics only for nests within my reach, I included measurements of height, distance and trunk diameter in a separate analysis to increase my sample size. I determined whether there were differences in nest site characteristics between sites by evaluating whether the 95% confidence interval of the effect size (Hedge's d) overlapped zero (Nakagawa and Cuthill 2007). I compared the relationship between nest site characteristics and daily survival rate (DSR) at each site using logistic

exposure models (Shaffer 2004). At each site, one model set included additive permutations of the fixed effects of height, distance and trunk diameter. A second model set included additive permutations of PC1 and PC2.

To determine whether reused nests had a higher probability of fledging than newly built nests, I modelled DSR as a function of a single categorical fixed effect coding whether the nest was reused or newly built. I did this analysis separately for each site: 1) for all reused nests, 2) only including reused nests that had fledged young in the first attempt and 3) only including reused nests that failed due to presumed depredation of the first attempt. I performed the latter analysis only for nests on Rota, due to the small sample size of reused nests following depredation in Australia. Finally, I determined the repeatability of the maximum age (days after clutch initiation) reached during subsequent attempts at the same nest site using linear mixed models (Nakagawa and Schielzeth 2010). For unsuccessful nests, I recorded the maximum nest age as the age on the day the nest was first observed empty. For successful nests, I used the modal fledging age at each site (29 days on Rota and 27 days in Australia) as the maximum age. I excluded nest reuse following hatching failures from the repeatability analyses.

RESULTS

Nest Site Characteristics

In Australia, the most common nest tree species were *Mischocarpus pyriformis* (58%) and *Syzygium leuhmannii* (12%). Fantails built the remaining 30% of nests in *Acmena hemilamprum*, *Cupaniopsis anacardioides*, *Pittosporum* spp., *Drypetes deplanchei*, *Eupomatia laurina*, *Smilax australis*, *Cissus sterculiifolia* and various dead vine and tree species. On Rota, the most common nest tree species were *Eugenia* spp. (39%), *Guamia*

mariannae (27%) and *Triphasia tripholia* (22%). Fantails built the remaining 12% of nests in *Ochrosia mariannensis*, *Cynometra ramiflora*, *Psychotria mariana, Ficus prolixa*, *Ficus tinctoria*, *Maytenus thompsonii* and various dead vine and tree species.

Nest placement averaged 157% higher, 83% further from the trunk and in trees with 100% larger trunk diameter in Australia than on Rota (Table 3.1). PCA identified two orthogonal components that explained 58% of the variance in nest site measurements (Table 3.2). Nests in Australia tended to have higher PC1 and PC2 scores than nests on Rota (Table 3.1, Fig. 3.1). Nest site characteristics did not explain variation in DSR at either site, as indicated by the high ranking of the null model in all candidate sets (Table 3.3). On Rota, the only model ranked higher than the null model contained the fixed effect of trunk diameter. However, trunk diameter was unrelated to DSR (β = -0.07, 95% CI: -0.15, 0.02). In Australia, the only model ranked above the null model contained the fixed effect of PC1. However, PC1 score did not predict DSR (β = 0.13, 95% CI: -0.03, 0.31).

Nest Reuse

In Australia, fantails reused nests following fledging (N = 19), hatching failure (N = 3) and presumed depredation (N = 1), plus one instance where the fate of the first nest was unknown. On Rota, I observed nest reuse after fledging (N = 18), presumed depredation (N = 15) and hatching failure (N = 1), plus two instances where the fate of the first nest was unknown. On Rota, there were three instances of a nest being used three times in a single breeding season, whereas in Australia I only observed nests being used twice.

I located 72 newly built nests (23% of all nests found) in Australia and 46 newly built nests (15% of all nests found) on Rota. Whether a nest was reused or newly built did

not predict daily survival rate in Australia (β = 0.28, 95% CI: -0.36, 0.86) or on Rota (β = 0.03, 95% CI: -0.69, 0.71). Reused nests following fledging did not have a higher daily survival rate than newly built nests in Australia (β = -0.15, 95% CI: -0.80, 0.60) or Rota (β = 0.21, 95% CI: -0.60, 1.10). There was a trend for reused nests following presumed depredation to have a lower daily survival rate than newly built nests on Rota (β = -0.68, 95% CI: -1.40, 0.16). Maximum age attained in subsequent attempts at the same nest site was neither repeatable in Australia (R = 0.00, 95% CI: 0.00, 0.52) nor on Rota (R = 0.05, 95% CI = 0.00, 0.45).

DISCUSSION

I observed a significant difference in nest site characteristics between Australia and Rota. Fantails built nests higher above ground, further from the trunk of the nest tree and in trees with larger trunk diameter in Australia than on Rota. It is possible that this variation in nest site characteristics results from adaptive differences in nest site selection between sites due to the high risk of nest predation by reptiles in Australia (Chapter 1). However, these differences may also reflect the forest structure of my study sites. For example, the canopy is approximately three times taller at my Australian site than on Rota and the well-developed sub-canopy in Australia may provide better nesting habitat than the relatively sparse shrub layer. On Rota, the canopy is storm-pruned (average height < 10 m) and the dense understory shrub layer appears to provide the best nesting habitat for fantails. Brown treesnakes are detected in all forest strata on Guam, including the shrub layer (Rodda 1992, Tobin et al. 1999). Therefore the lack of nest site refugia on Guam could have contributed to fantails' rapid decline following brown treesnake introduction (Savidge 1987).

Nest site characteristics did not predict DSR at either study site. Latent nest site characteristics did not appear to influence fantail nest survival: reused nests following fledging did not have a higher DSR than newly built nests and nest fate was not repeatable for reused nests. Sachtleben (2005) also did not find a relationship between nest site characteristics and fantail DSR on the island of Saipan (115 km from Rota). Thus, depredation of fantail nests seems to occur randomly with respect to nest sites and may instead arise incidentally due to variation in predator spatial behavior (Vickery et al. 1992, Hammond 2016).

Additionally, it may be impossible for birds to choose a nest site that is safe from all potential predator species (Remeš 2005, Colombelli-Négrel and Kleindorfer 2009). Contemporary nest site characteristics may thus maximize reproductive success despite being uncorrelated with nest survival (Latif et al. 2012). Some previous research suggests that climbing predators target nests that are more easily accessible (e.g. Conkling et al. 2012, Sperry et al. 2012). However, lace monitors (the principal nest predator at my Australian site, Chapter 1) preyed upon nests located 1.20 to 5.79 m above ground, up to 2.50 m from the trunk of the tree and with a supporting branch diameter as small as 4.63 mm. This suggests that fantail nest sites do not provide refuge from climbing predators in Australia.

Fantails at both sites tended to reuse nests more often following fledging, as has been observed in other species (Styrsky 2005, Ellison 2008). In Australia, only 4% of reused nests occurred following presumed depredation during the first nest attempt. By contrast, 44% of reused nests occurred following presumed depredation on Rota. Predators were the most common cause of nest failure at both sites (Chapter 1), therefore

it is unlikely that this difference is due to failures from other causes on Rota. Instead, fantails may have an innate predisposition to reuse nests that is refined through experience. While I observed similar DSR between reused nests following fledging and newly built nests, reused nests following presumed depredation tended to have lower DSR. A majority (60%) of reused nests following presumed depredation on Rota occurred during my 2017 field season, 16-20 months after the island experienced a category 3 typhoon. Typhoon activity is inversely related to fantail detection rates on Rota (Ha et al. 2012), indicating that typhoons may cause adult mortality. If this is the case, my 2017 field season may have been characterized by a higher proportion of young breeders, which could explain the relatively high frequency of nest reuse following predation. Future studies should investigate the ontogeny of nest reuse behavior in fantails and other species known to reuse nests.

Ellison (2008) found that reused Vermillion Flycatcher nests had a higher DSR than newly built nests. However, reused and newly built nests have equal survival rates in other species (Styrsky 2005, Redmond et al. 2007, present study). Therefore, nest reuse may represent an energy- and/or time-saving strategy (Cavitt et al. 1999, Styrsky 2005, Ellison 2008) or may result from nest-site limitation (Redmond et al. 2007). It is unlikely that nest reuse reflects nest site limitation in my study system, because fantails rarely reused nest sites in subsequent years (2 nests in Australia, 2 nests on Rota). However, fantails likely saved time and energy by reusing an existing nest structure, since nest-building generally requires 7-10 days (L. Nietmann, personal observation). Nest reuse appears to be relatively common in flycatchers (Ellison 2008). Aerial insectivores' longer nesting cycle (Remeš 2007) and/or the sensitivity of their food supply to environmental

variation (Davies 1977, Murphy 1983, 1989) may increase the need for saving time and/or energy for future breeding attempts. Future studies should investigate the costs and benefits of nest reuse in other species in order to better understand the adaptive value of this behavior.

Nest site characteristics are likely shaped by selection pressures in concert with, or in addition to, nest predation (e.g. adult survival). While there is ample evidence for plasticity, learning and rapid evolution of nest site characteristics (Hatchwell et al. 1999, Zanette et al. 2011, Vanderwerf 2012), if nest sites expose females to high predation risk during incubation, population decline may preempt adaptive changes in nest site selection. Nocturnal predation of incubating females likely contributed to the extirpation of fantails on Guam following brown treesnake introduction. The storm-pruned forest structure on Guam may also have amplified the high density of brown treesnakes compared to the snakes' native range, by concentrating snakes in the strata in which fantails nest. Given the limited diversity of nest sites for forest birds in the Mariana Islands, all possible efforts should be made to prevent future introductions of non-native predators.

FIGURES

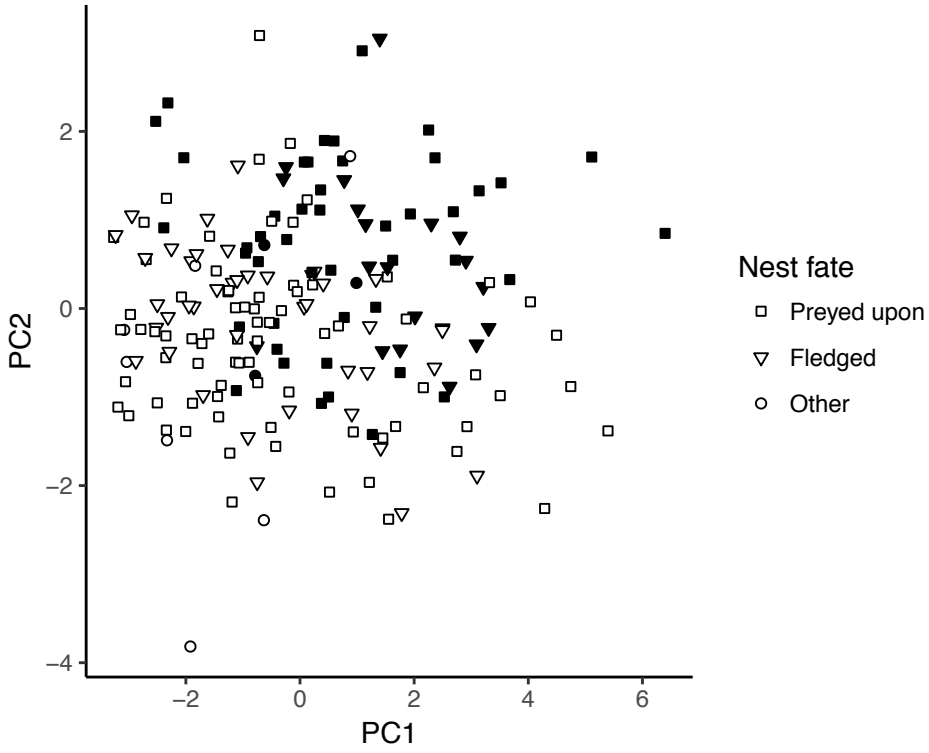

Figure 3.1. Nests in Australia (filled symbols) have higher PC1 and PC2 scores than nests on Rota (open symbols), but PC scores are not related to nest fate at either site. 'Other' nest fates include failure due to hatching failure or weather, or a nest that was not monitored to completion.

TABLES

Table 3.1. Mean (range) measurements of nests in Australia and Rota.

	Australia	**Rota**	**Effect size**	**95% CI[1]**
Height (m)	4.09 (0.92, 10.0)	1.59 (0.45, 4.34)	**1.83**	**1.60, 2.06**
Distance (m)	1.19 (0.00, 3.50)	0.65 (0.08, 2.25)	**1.02**	**0.80, 1.25**
Trunk diameter (cm)	7.10 (0.54, 29.70)	3.54 (0.90, 17.83)	**0.92**	**0.69, 1.14**
Branch distance (m)	1.17 (0.12, 2.45)	0.79 (0.00, 2.56)	**0.77**	**0.47, 1.08**
Branch length (m)	1.61 (0.44, 3.27)	1.27 (0.39, 3.30)	**0.63**	**0.33, 0.94**
Support diameter (mm)	6.46 (3.59, 18.79)	6.38 (4.02, 11.21)	0.04	-0.25, 0.34
Branch diameter (mm)	14.84 (3.85, 29.23)	12.32 (4.85, 29.40)	**0.46**	**0.16, 0.76**
Paths	1.13 (0, 4)	1.72 (0, 5)	**-0.51**	**-0.75, -0.27**
Branchlets	3.42 (2, 6)	3.54 (2, 6)	-0.17	-0.41, 0.07
PC1	0.98 (-3.18, 5.07)	-0.54 (-3.26, 6.35)	**0.81**	**0.50, 1.11**
PC2	0.64 (-2.29, 2.95)	-0.35 (-3.76, 3.06)	**0.95**	**0.64, 1.26**

[1]95% CIs around the effect size, Hedge's d. Bold values indicate confidence intervals that do not overlap zero.

Table 3.2. Principal component analysis loadings of nest site variables. Bold values indicate loadings > 0.30.

Parameter	**PC1**	**PC2**
Height	0.19	**0.49**
Distance	**0.47**	-0.02
Trunk diameter	**0.32**	0.09
Branch distance	**0.48**	-0.04
Branch length	**0.46**	-0.05
Support diameter	0.03	**0.33**
Branch diameter	**0.41**	0.00
Paths	0.17	**-0.60**
Branchlets	-0.03	**-0.53**
Eigenvalue	3.99	1.24
Variance explained (%)	44.40	13.80
Cumulative variance explained (%)	44.40	58.20

Table 3.3. Candidate models for the relationship between nest site characteristics and daily survival rate in Australia and Rota. For each site, the first set of candidate models include all nests and the second candidate includes nest sites that were measured in more detail due to their accessibility (i.e. had complete observations that could be reduced using PCA).

	Fixed effects[1]	k	AIC_c	ΔAIC_c	AIC_c weight	Log likelihood
Australia	null	1	1004.53	0.00	0.37	-501.27
	H	2	1006.33	1.80	0.15	-501.17
	D	2	1006.44	1.91	0.14	-501.22
	T	2	1006.44	1.91	0.14	-501.22
	H + D	3	1008.32	3.79	0.06	-501.16
	H + T	3	1008.33	3.80	0.06	-501.16
	D + T	3	1008.41	3.88	0.05	-501.20
	H + D + T	4	1010.33	5.8	0.02	-501.16
	PC1	2	355.79	0	0.41	-171.77
	Null	1	348.03	0.47	0.32	-173.01
	PC1 + PC2	3	349.57	2.01	0.15	-171.77
	PC2	2	350.04	2.47	0.12	-173.01
Rota	T	2	521.23	0.00	0.28	-258.61
	null	1	521.84	0.62	0.20	-259.92
	D + T	2	522.72	1.49	0.13	-258.35
	H + T	2	523.01	1.78	0.11	-258.49
	H	2	523.27	2.04	0.10	-259.63
	D	2	523.83	2.60	0.08	-259.91
	H + D + T	4	524.34	3.11	0.06	-258.14
	H + D	3	525.17	3.94	0.04	-259.57
	Null	1	491.53	0	0.51	-244.76
	PC2	2	493.32	1.79	0.21	-244.65
	PC1	2	493.34	1.81	0.2	-244.66
	PC1 + PC2	3	495.22	3.69	0.08	-244.59

[1]H = height, D = horizontal distance from trunk, T = trunk diameter, PC1/PC2 = first/second principal component

Chapter 4: Site-specific incidence of band-related injuries in Rufous Fantails

INTRODUCTION

Bird banding has transformed my understanding of avian ecology by elucidating patterns of movement, life history and social behavior. As such, the benefits of banding to science are believed to outweigh the risks of injury to banded birds. However, for those species that experience band-related injuries, banding presents both ethical and scientific concerns, since an injury can impact behavior, reproduction, and survival (Sedgwick and Klus 1997). Band-related injuries include foot entrapment (Berggren and Low 2004, Griesser et al. 2012), tarsal swelling (Rothstein 1979, Splittgerber and Clarke 2006, Pierce et al. 2007), inflammation (Griesser et al. 2012), abrasion (Lingle et al. 1999, Berggren and Low 2004, Freifeld et al. 2016), and necrosis and amputation of the foot (Sedgwick and Klus 1997, Amat 1999, Lingle et al. 1999, Pierce et al.2007, Hache et al. 2016).

Flycatchers banded with plastic color bands appear to be especially susceptible to injuries. In six intensively studied species, injury rates of color-banded flycatchers ranged from 9.6 to 35.3% of banded birds, with injuries occurring most often when birds were banded with two plastic bands on the same leg (Sedgwick and Klus 1997, Pierce et al. 2007). Band-related injuries have also been reported for Ochre-bellied Flycatchers (*Mionectes oleaginous*, Koronkiewicz et al. 2005), Leaden Flycatchers (*Myiagra rubecula*, S. Tremont, personal communication), and some *Empidonax* and *Contopus* species (Haas and Hargrove 2003), indicating that ecology or tarsal morphology may

predispose flycatchers to band-related injuries. Although leg injuries in other passerines have been attributed to ill-fitting bands (Splittgerber and Clarke 2006, Griesser et al. 2012), in several flycatcher species the plastic band material itself appears to cause injuries (Koronkiewicz et al. 2005, Pierce et al. 2007).

Splittgerber and Clarke (2006) found that, unlike metal bands, both celluloid and Darvic plastic color bands generate static electricity, which can attract shed tarsal scales and other debris. Leg injuries occur when debris becomes lodged beneath the bands, causing swelling and eventual constriction and amputation of the foot (Splittgerber and Clarke 2006, Pierce et al. 2007). Griesser et al. (2012) found that leg injuries in Purple-crowned Fairy-wrens (*Malurus coronatus*) seemed to be caused by spider web accumulation under the bands. Using colored metal bands instead of plastic bands is a recommended method for reducing the prevalence of band-related injuries in Purple-crowned Fairy-wrens, and has also been successfully implemented in several other species (Koronkiewicz et al. 2005, Pierce et al. 2007, Griesser et al. 2012). Here, I report observations of band-related leg injuries caused by spider web accumulation in a Rhipidurid flycatcher, the Rufous Fantail *Rhipidura rufifrons*, and make recommendations for future color-banding studies in this and related species.

METHODS

I studied two Rufous Fantail (hereafter 'fantail') subspecies: *R. r. mariae* on the island of Rota, Commonwealth of the Northern Mariana Islands, USA (hereafter 'Rota,' 14°09'04" N, 145°12'54" E) and *R. r. rufifrons* in Iluka Nature Reserve (NSW), Australia (hereafter ',' 29°24'19" S, 153°21'34" E). Rota is a raised limestone island of volcanic origin, which experiences a tropical climate year-round (average high temperature: 28 – 30 °C).

This island receives most of its 244 cm of annual rainfall between July and January (NOAA 2017). My Australian site is the largest remnant of littoral rainforest in New South Wales. This site receives an average of 146 cm of rain per year, most of which falls between December and March, and experiences a sub-tropical climate with average summer temperatures of 20 – 26 ºC (Grantley 2010). On Rota, fantails are resident breeders that occupy stable, year-round territories. They breed throughout the year, with a distinct peak in nesting between February and June (personal observation). In Australia, fantails occupy breeding territories between September and February before migrating to over-winter in the tropics (Higgins et al. 2006).

At both study sites, I captured fantails using mist nets (Avinet, Portland, USA). The first time a bird was captured, I measured tarsus length using digital calipers (precision = 0.01 mm), mass using a digital scale (precision = 0.01 g), and wing chord (flattened) and tail length using a ruler to the nearest 0.5 mm. I determined sex based on the presence of a brood patch (females) and/or the orientation of the cloacal protuberance (caudal orientation = female). I confirmed this method of sexing by observing copulations between color-banded fantails.

Rota

In 2013-2014, I banded fantails on Rota with a unique combination of size XF Darvic plastic color bands (Avinet, Portland, USA; height x internal diameter = 4.0 x 2.3 mm) and a size 0 United States Geological Survey (USGS) numbered aluminum band (5.5 x 2.1 mm). I use the phrase 'plastic color bands' to refer to the banding scheme in which I placed a USGS metal band on one tarsus with a color band above it and placed two color bands on the other tarsus.

After re-sighting plastic color-banded birds with leg injuries (Fig. 4.1) in April 2014, I ceased color-marking and aimed to recapture color-banded birds. For all recaptured birds, I evaluated the severity of injuries using a six-point rating scale (Table 4.1), from 0 (clean, healthy tarsus) to 5 (leg amputation). I evaluated stage 3-5 injuries by visual inspection of recaptured birds or during observations of free-flying individuals (see 're-sighting' below). Stage 0-2 injuries could only be evaluated by capturing birds and inspecting their tarsi.

In 2014, I elected to remove all bands (USGS and plastic) from re-captured individuals that had sustained a significant injury (stage 3-5, Table 4.1) that was considered to be due to the presence of the bands. For the remaining individuals, I removed any accumulated debris using forceps and removed only the plastic bands. These individuals were then banded with a single 'pin-striped' aluminum band (Fig. 4.1A, Koronkiewicz et al. 2005), on the leg opposite the USGS band. I made pin-striped bands by wrapping a plain aluminum band (National Band and Tag, Newport, USA; 5.5 x 2.1 mm) with strips of automotive pin-striping and coating the resulting colored band in clear epoxy (Koronkiewicz et al. 2005). My method for making the pin-striped bands departed from Koronkiewicz et al. (2005) in that I used five-minute epoxy rather than flexible rod-wrapping epoxy due to the unavailability of the latter on Rota. I use the phrase 'pin-striped color bands' to refer to the banding scheme in which fantails were banded with a pin-striped color band on one tarsus and a numbered metal band on the other tarsus.

In 2015, I observed injuries caused by pin-striped color bands, thus I elected to terminate banding efforts. In 2015 and 2017 I aimed to recapture all remaining banded fantails in order to remove their bands and did not band any additional fantails.

Australia

From 2014 to 2016 I banded adult fantails with a size 01 Australian Bird and Bat Banding Scheme (ABBBS) aluminum-magnesium alloy band (5.5 x 2.0 mm) on one tarsus and the other tarsus with the same pin-striped bands that I used on Rota. To increase the number of unique color combinations, ABBBS bands were anodized in gold, red, or blue by Australian Anodizing (Goonellabah, NSW) or were left un-anodized. In 2015 and 2016 I recaptured a total of 14 individuals to assess the prevalence of band-related injuries. I did not band any fantails with plastic color bands in Australia. I did not remove bands from any fantails in Australia, because I never observed any band-related injuries at this site.

Re-sighting

I re-sighted fantails six days per week for a total of 38 weeks on Rota (1 week in 2013, 12 weeks in 2014, 14 weeks in 2015 and 11 weeks in 2017) and 33 weeks in Australia (five weeks in 2014, 12 weeks in 2015 and 16 weeks in 2016). During each sighting of a banded bird, I used binoculars to note whether the bands were moving freely on each tarsus and observed behavior to confirm that the bird could perch on both legs.

Data Analysis

I used t-tests to compare body size measurements of males and females within each site and overall body size measurements between sites. I compared Kaplan-Meier survival curves between sites using a Cox proportional-hazard model (Therneau and Grambsch

2000). Data were right-censored at the last time I re-sighted each individual, or uncensored for cases of band removal. I included re-sighting effort (measured in weeks of field work after initial banding) as a covariate to account for any differences in effort between sites or years. For birds that had their bands removed, I only counted re-sighting effort for the duration they were banded.

In addition to the injury scale (Table 4.1), I also used the banding hazard scale proposed by Griesser et al. (2012) to facilitate comparison of injury prevalence and severity with other species for which band-related injuries have been reported. I used chi-square tests to compare: 1) the proportion of all captured individuals that had stage 1 injuries at the time of initial capture versus after wearing bands for at least 35 days at each site and 2) the proportion of individuals that had stage 1 injuries at the time of initial capture between sites. Since I removed all debris from the tarsi of every fantail I captured, these comparisons allowed us to determine whether bands augmented the accumulation of spider webs around the tarsus and whether the natural level of spider web accumulation differed between Rota and Australia. All statistical analyses were performed in R 3.4.1 (R Core Team 2017).

RESULTS

I captured 81 fantails in Australia (25 females, 48 males and 8 of unknown sex) and 69 fantails on Rota (24 females, 35 males and 10 of unknown sex). Males had larger body size measurements than females in both Australia and Rota (Table 4.2). Fantails in Australia were heavier and had longer wings and tails, but shorter tarsi than fantails on Rota (Table 4.2). Fantails survived for a median of 346 days (95% CI: 323, 438) in

Australia and 300 days (95% CI: 255, 392) on Rota. There was no difference in survival between sites (z = -1.01, P = 0.31).

Rota

Plastic color bands

Of the 24 fantails banded with plastic color bands on Rota in August 2013, I re-sighted 16 individuals (66.7 %) in April 2014. I banded an additional 15 fantails with plastic color bands in 2014 before my first re-sighting of an injured bird, making a total of 31 plastic-banded individuals on my study plot in 2014, 24 of which I was able to re-capture. Based on field observations of all re-sighted individuals, and in-hand evaluation of re-captured birds, 10 of 31 individuals (32.3%) had significant band-related injuries (stage 3-5, Fig. 4.2A), giving a hazard rating of 3.39 (Table 4.1). Restricting my analysis to include only birds that had worn bands for at least six months revealed a higher prevalence of stage 3-5 injuries (37.5%, Fig. 4.2A) and a hazard rating of 5.19. Stage 3-5 injuries were more common on the leg banded with two plastic color bands (7 of 10 individuals). Sixteen re-captured individuals (66.7%) had stage 1 or 2 injuries, which I believe would eventually progress to a severe injury if the bands were not removed. Four re-captured birds (16.7%) had neither an injury nor accumulated debris. It is likely that these figures are an underestimate of the prevalence of band-related injuries because stage 1-3 injuries could only be detected with certainty among re-captured birds.

Of the five individuals whose injuries affected their ability to perch (stage 4-5), two males attended active nests but disappeared shortly after nest failure, two males were unpaired and one female was paired but did not initiate a nest despite constant harassment from her mate (males chase females aggressively prior to initiation of nest-building). One

of the unpaired males sustained a stage 4 injury within 68 days of banding (Fig. 4.2A). All five severely injured individuals were shy and generally unresponsive to my re-capture efforts and three of them disappeared before I was able to remove their bands.

Pin-striped color bands

I banded 40 fantails in 2014 with pin-striped color bands: 20 were individuals whose plastic color bands were replaced with a pin-striped band and 20 were captured and banded for the first time. Of these, 25 (62.5%) were re-sighted in 2015 and 8 (20%) of the birds re-sighted in 2015 were also re-sighted in 2017. In 2014, I recaptured a female with pin-striped bands that sustained a stage 3 injury within 53 days of her initial banding (i.e. she was never banded with plastic bands). Due to the rapid development of this injury, I elected to terminate banding efforts on Rota. During 2014 - 2017, I recaptured 17 of 25 re-sighted individuals to remove their pin-striped and USGS bands: two had stage 3 injuries (11.7%), 14 had stage 1 or 2 injuries (82.4%), and one had neither injury nor accumulated debris (Fig. 4.2B), yielding a hazard rating of 0.12. Despite the trend for pin-striped bands to reduce the severity of injuries (Fig. 4.2), birds with pin-stripe bands ($N = 16$) were more likely to have spider web accumulation on their tarsus than unbanded birds ($N = 17$, $X^2 = 5.02$, df = 1, $P = 0.025$).

Australia

Of the 60 birds banded in 2014 with pin-striped color bands, I re-sighted 43 (72%) in 2015 and 26 (43%) in 2016. Of the birds re-sighted in 2015, 26 (43%) were re-sighted in 2016. I banded an additional 11 birds in 2015, 8 (73%) of which were re-sighted in 2016. During re-sighting, I did not observe evidence of stage 3-5 injury in any individual. Among re-captured fantails, I did not observe any instances of stage 2-5 injury and 4 of

14 (28.6%) individuals had a stage 1 injury. Despite the apparent low risk of band-related injury in this population, banded individuals ($N = 14$) were more likely to have spider web accumulation on their tarsi than unbanded birds ($N = 79$, $X^2 = 5.64$, df = 1, $P = 0.018$), indicating that banding may elevate the risk of leg injuries. Unbanded fantails in Australia ($N = 79$) were less likely to have tarsal spider web accumulation than unbanded fantails on Rota ($N = 17$, $X^2 = 23.45$, df = 1, $P < 0.001$).

DISCUSSION

My observations suggest that fantails on Rota are highly sensitive to banding with plastic color bands. The rapid development of injuries (< 3 months, Fig. 4.2A) is also indicative of fantails' susceptibility—band-related injuries in less sensitive species appear 1-3 years after banding (Sedgwick and Klus 1997, Splittgerber and Clarke 2006, Hache et al. 2016, but see Armstrong et al. 1999, Lingle et al. 1999, Pierce et al. 2007, Griesser et al. 2012 for descriptions of injuries occurring after 2-12 weeks). Although there are reports of successful breeding following leg loss in other species (i.e. stage 4-5 injury, Lingle et al. 1999, Pierce et al. 2007, Hache et al. 2016), none of the five fantails in this injury category bred successfully and only two initiated a nest. Thus, in addition to being among the species most susceptible to band-related injuries, the fitness consequences to injured fantails may be high.

While switching from plastic to pin-striped color bands reduced the injury rate on Rota (Fig. 4.2), fantails still experienced injuries while wearing pin-striped bands (hazard rating = 0.12, Fig. 4.2B). For comparison, a hazard rating of 0.11 was sufficient for researchers to switch from plastic to metal bands in Purple-Crowned Fairy Wrens *Malurus coronatus* due to ethical concerns (Griesser et al. 2012). Therefore, my

observations suggest that banding per se may constitute a significant risk to fantails on Rota. Improperly fitting bands cause injuries in other species (e.g. Splittgerber and Clarke 2006, Griesser et al. 2012), but did not appear to cause injuries in fantails. On Rota, an average of 73.2% of the metal band's internal diameter (66.8% of the plastic band's internal diameter) was occupied at the midpoint of the tarsus, which is within the suggested range for small passerines (Griesser et al. 2012).

Instead, my observations suggest that bands promote the accumulation of spider web material, which eventually causes tarsal irritation and swelling (Fig. 4.1, see also Greisser et al. 2012). Splittgerber and Clarke (2006) found that plastic colour bands generate static charge, which causes them to attract more foreign material than metal bands. This might explain why I observed a higher incidence of severe injuries among fantails wearing plastic colour bands than fantails wearing pin-striped bands on Rota (Fig. 4.2). However, I also found that the presence of pin-striped bands appeared to increase the probability that a fantail would have a stage 1 (i.e. debris-only) injury, relative to previously unbanded birds. This indicates that the presence of bands—regardless of material—might interfere with a fantail's ability to remove debris from the tarsus. Additionally, interference with tarsal preening could reduce the application of uropygial gland secretions to the tarsus, which have been shown to have anti-microbial properties *in vitro* (Moreno-Rueda 2017). The fact that reducing the proportion of tarsus length covered by bands decreased injury rates in other species (Haas and Hargrove 2003, Amirault et al. 2006) provides further support for the idea that bands restrict access to the tarsus.

Variation in how often fantails encounter spider webs could explain the different injury rates between my study sites (Fig. 4.2). I rarely captured unbanded birds with spider webs on their tarsi in Australia (5.1% of captures), but this was a common occurrence on Rota (52.9% of captures). This result could be due to differences between my sites in the ambient density of spider webs (see Rogers et al. 2012 for quantification of spider web density on Rota). While I did not measure spider web density, I did observe fantails using spider webs to construct their nests at both sites. Fantails appear to use their feet to shape the nest cup (personal observation), which could explain how they accumulate spider webs on their tarsi. Year-round breeding on Rota, compared to seasonal breeding in Australia may influence accumulation of spider webs and other debris. However, Fantails in Australia still build 2 – 5 nests per year, suggesting that this explanation may not fully explain the differences between sites in injury risk. The possibility that longer tarsi (Table 4.2) somehow increased the probability of spider web accumulation is another potential explanation for the higher incidence of stage 1 injuries on Rota.

I do not think that differences in forest substrate (Lingle et al. 1999, Freifeld et al. 2016) or foraging behavior (Rose 1997, Berggren and Low 2004, Griesser et al. 2012) influenced the differences in band-related injuries between sites. My observations suggest that fantails use primarily aerial and gleaning foraging maneuvers at both my study sites and I did not observe any other differences in behavior that could explain the prevalence of band-related injuries on Rota. While differences in the material of the issued bands is a potential confounding variable (USGS bands were aluminum, ABBBS bands were alloy), fantails wore a pin-striped (i.e. aluminum) band on one tarsus at both sites. Therefore, if

differences between sites were caused by the material of the issued metal bands, I would expect to see twice as many injuries on Rota as in Australia, since fantails on Rota wore two aluminum bands on Rota and one aluminum and one alloy band in Australia. Instead, I found a more than three-fold difference in the prevalence of debris accumulation or injury (stage 1 – 5 injury) for fantails wearing pin-striped bands on Rota (94.1%) versus in Australia (28.6%; Fig. 4.2B, C). Although my sample size is small, this suggests that differences in the material of government-issued bands did not cause the differences in injury rates between my study sites.

Fantails in Australia are migratory and I only re-sighted newly banded fantails for a median of four weeks prior to migration each year. Thus, it is possible I underestimated the injury rate, if injuries prevented fantails from returning to my study site. However, other small, migratory passerines have successfully returned to breed after experiencing significant band-related injuries during the non-breeding season (Sedgwick and Klus 1997, Hache et al. 2016). Additionally, the proportions of banded birds I observed in subsequent years (72% and 73% in 2015 and 2016, respectively) are similar to those reported for other migratory and resident Australia forest birds (59 – 87%, Robinson 1990, Rowley and Russell 1991, Bridges 1994, van Dongen and Yocom 2005). Huggett (2000) found that < 40% of fantails banded with plastic color bands (Darvic size XF) returned in subsequent breeding seasons, but he did not observe any band-related injuries in two years of re-sighting and recapturing (A.J. Huggett, personal communication). It is unclear whether the difference in return rate between Huggett (2000) and the present study is due to re-sighting effort, habitat quality, or differences in injury rate mediated by band material. Regardless, my observations of significant band-related injuries on Rota,

combined with my small sample of recaptured fantails and limited re-sighting effort prior to migration in Australia, suggest that future studies should closely monitor banded populations of fantails and related species.

Conclusions

My research indicates that assessment of stage 1 injuries in unbanded birds may allow banders to forecast risks of injury in previously unstudied populations, at least for those species in which spider web accumulation influences injury development (e.g. Griesser et al. 2012). Additionally, I encourage future studies of the effects of life history on the prevalence of injuries in certain species (Pierce et al. 2007). For example, comparative studies examining whether the type of nest material used, breeding season length, and/or method of nest construction influences injury risk could allow *a priori* identification of at-risk species or populations. In the event that fantails are re-introduced to the island of Guam—where they were extirpated by an introduced snake (Savidge 1987)—I recommend extreme caution with banding efforts due to the high density of spider webs that has followed the extinction of nearly all forest birds (Rogers et al. 2012). Finally, developing alternative auxiliary markers for small passerines should be prioritized and piloted prior to attempting future color-marking of fantails on Rota.

FIGURES

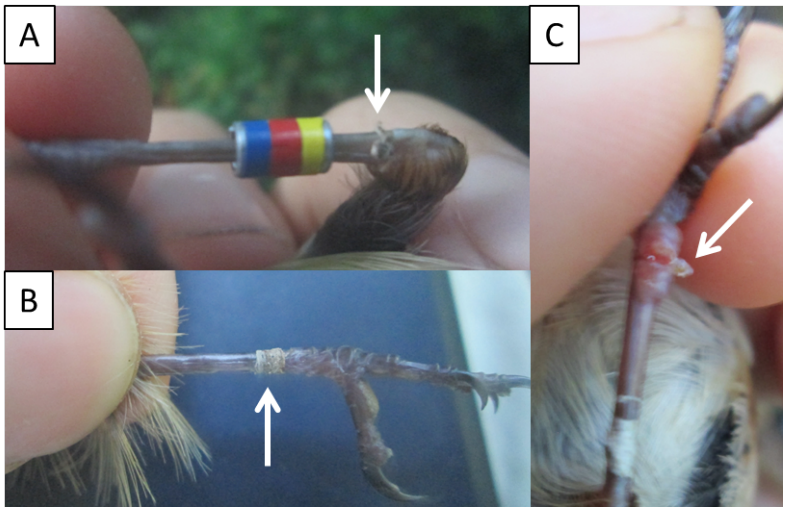

Figure 4.1. Progression of band-related injuries in Rufous Fantails. A) A loose bracelet of spider webs forms around tarsus (above a 'pin-striped' aluminum band), B) the bracelet adheres to the tarsus as more spider webs accumulate and C) swelling occurs under the band and spider web bracelet cuts into the tarsus causing eventual amputation of the foot (not shown).

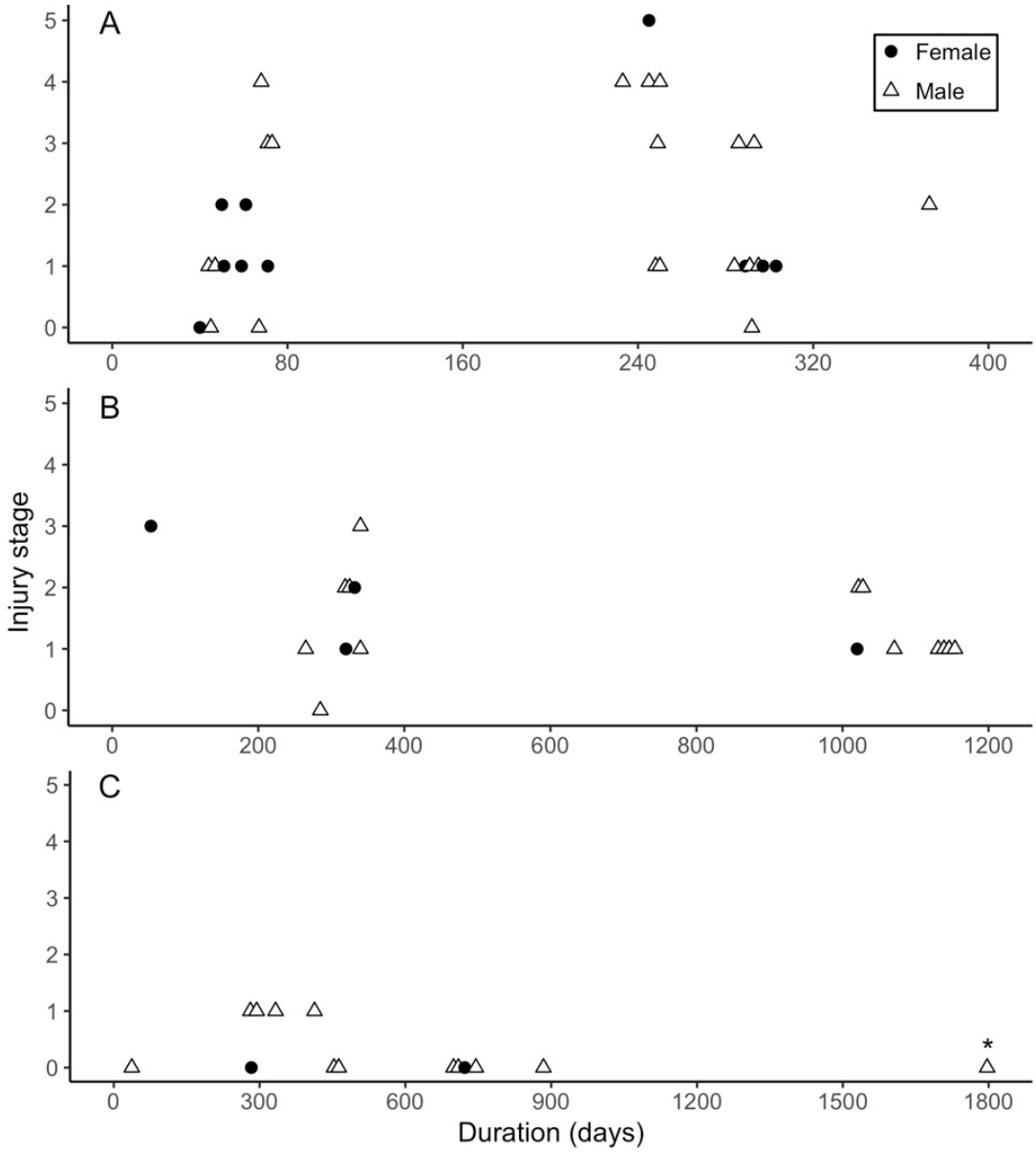

Figure 4.2. Band-related injuries were most severe among Rufous Fantails wearing plastic bands on Rota (A), intermediate among Fantails wearing metal bands on Rota (B) and rare among Fantails wearing metal bands in Australia (C). Injury stage corresponds to the rating scale described in Table 4.1, where 0 indicates no injury and 5 indicates complete amputation of the foot. Overlapping points have been horizontally offset. Note the different x-axis scales. *Initially captured in 2010 by a different bander.

TABLES

Table 4.1. Rating scale used to assess the severity of band-related injuries.

Stage	Hazard points[1]	Description
0	0	No injury or accumulation of material
1	0	Loose bracelet(s) of spider web material around tarsus
2	0	Spider webs wound tightly and adhered to tarsus
3	1	Swelling under and around bands
4	20	Loss of use of foot (difficulty perching)
5	20	Amputation of foot

[1]See Griesser et al. (2012) for a description of the banding hazard rating scale.

Table 4.2. Mean (SE) body measurements of male and female Rufous Fantails in Australia and Rota. Statistically significant differences between males and females within each site and the overall difference between sites are indicated in the P_{sex} and P_{site} columns, respectively.

	Australia				**Rota**				
	Female	**Male**	P_{sex}	**Overall**	**Female**	**Male**	P_{sex}	**Overall**	P_{site}
Tarsus (mm)	20.95	21.63	***	21.39	21.55	22.14		21.90	
	(0.10)	(0.08)		(0.07)	(0.08)	(0.07)	***	(0.06)	***
Wing (mm)	70.32	74.34	***	72.96	64.92	67.92		66.69	
	(0.34)	(0.29)		(0.29)	(0.25)	(0.19)	***	(0.23)	***
Tail (mm)	82.88	85.80	***	84.79	77.14	78.75		78.10	
	(0.45)	(0.34)		(0.29)	(0.45)	(0.29)	**	(0.26)	***
Mass (g)	9.08	9.90	***	9.64	8.50	8.86		8.74	
	(0.09)	(0.06)		(0.07)	(0.14)	(0.07)	*	(0.07)	***

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

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