

A RARE CASE: HABITAT SPECIALISATION AND COOPERATIVE BREEDING FACILITATES THE PERSISTENCE OF AN UNDERSTORY INSECTIVORE IN RAINFOREST FRAGMENTS

*Pale-yellow Robin (*Tregellasia capito*)*



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This thesis submitted by Renée Jean Cassels in partial fulfilment of the requirements for the Degree of Bachelor of Science with Honours in the College of Science & Engineering of James Cook University.

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ABSTRACT

Habitat loss and degradation are among the greatest threats to biodiversity. The negative effects of fragmentation include disruption of ecosystem services, changes in community composition and species interactions, population dynamics, genetic diversity, individual fitness and dispersal. Within rainforest communities, understory insectivores are disproportionately impacted due to high habitat specificity, low mobility, and greater reliance on the forest interior than other passerine guilds. Consequently, populations are declining globally. However, habitat fragmentation is not negative for all species. The Pale-yellow Robin (PYR) *Tregellasia capito* is a territorial, understory insectivore known to inhabit continuous forest and small fragments where other species have been lost. Based on a review of the literature I developed two principal hypotheses to explain this. First, habitat fragmentation, while not immediately detrimental, may become problematic in the long term due to the effects of post-fragmentation crowding. Second, habitat fragmentation does not have a negative impact on the species owing to certain species-specific traits that confer protective or competitive advantages (i.e. cooperative breeding, habitat specialisation, and competitive exclusion). Based on the weight of evidence in the literature, I predicted the first hypothesis would be true. Thus, the initial aim of my study was to test the first hypothesis. To do this, I designed a nested study comprised of four fragment-size classes, each with four rainforest sites on the Atherton Tablelands: >501 ha, >51 ha to 500 ha, 26–50 ha, ($n = 16$). ≥ 16 territories were surveyed in each class ($n = \geq 64$). Sites were all classified as Type 5a – Complex notophyll vine forest. To detect post-fragmentation crowding, PYR breeding territories were mapped and territory defence behaviour was recorded. Comparisons were then made between fragment-size classes to detect differences in PYR population densities, territory characteristics, and behaviour, resulting from a reduction in overall fragment size. Contrary to the literature, PYR populations were found to be indifferent to habitat fragmentation,

and able to persist in fragments with no significant changes to their population densities, territory characteristics, or territory defence behaviour. Thus, the second hypothesis was tested. Group size was used to gauge the incidence of cooperative breeding. Comparisons were then made between fragment-size classes. Spot-sampled habitat surveys ($n = 112$) were conducted and 15 habitat variables were measured. The relationship between PYR presence / absence and habitat variables was assessed to detect habitat specialisation. My results showed PYRs to be a disturbed habitat specialist, with the ability to utilise a cooperative breeding strategy to maximise use of preferred habitat. As such, this presented a new and rare case of habitat specialisation facilitating post-fragmentation persistence of a rainforest understory insectivore. Based on this, it was concluded that habitat fragmentation was not an existential threat to PYR populations in the Wet Tropics.

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GENERAL INTRODUCTION

Habitat fragmentation

Habitat loss and degradation are currently among the greatest threats to biodiversity globally, and are likely to remain major threats for decades to come (Fahrig 2003, Ewers & Didham 2006, Sodhi et al 2011, Newbold et al 2014, Freeman et al 2015, FAO 2016). Total global forest area has declined by 129 million ha (3.1%) over the last 25 years and the majority of this loss has been in the tropics, where human populations are still growing rapidly (FAO 2016). The primary causes of deforestation and loss of other habitats are agricultural expansion, followed by urbanisation and logging (Sodhi et al 2011, FAO 2016). Habitat fragmentation is a pervasive feature of modern landscapes (Bender et al 1998, Fahrig 2003, Ewers & Didham 2006, Newbold et al 2014, Bregman et al 2015). It is defined as a landscape-scale process whereby changes in habitat configuration result from a breaking up of habitat, independent of habitat loss (Fahrig 2003). Four separate drivers are characteristic of habitat fragmentation – reduction in total habitat amount, increase in the number of patches, decrease in overall size of patches, and increase in isolation of patches (Fahrig 2003, Ewers & Didham 2006). Critically, these drivers often interact synergistically with climate change, human-altered disturbance regimes, species interactions, and other drivers of population decline to magnify the impacts of fragmentation (Laurance et al 2002, Ewers & Didham 2006, Catterall et al 2008, Freeman et al 2015).

The negative effects of fragmentation have been shown to include disruption of ecosystem services (Hooper et al 2012, Bregman et al 2015, Peter et al 2015), changes in community composition and species interactions (Stouffer & Bierregaard 1995, Ford et al 2001, Maas et al 2009, Newbold et al 2014, Bennett et al 2015), population dynamics and genetic diversity (Bender et al 1998, Visco et al 2015) and individual fitness and dispersal (Hoffman & Hercus 2000, Şekercioğlu

et al 2002, Bonier et al 2009, Creel et al 2013). All of these factors can independently and/or concurrently contribute to the risk of local, regional or global extinction of species (Hausmann 2004, Ewers & Didham 2006, Ferraz et al 2007, Freeman et al 2015). Often, the full extent of these impacts on communities, populations, and species is not evident for many decades after the start of disturbance (Warburton 1997, Ford et al 2001, Moloney 2005, Ewers & Didham 2006, Sodhi et al 2011, Korfanta et al 2012, Visco et al 2015).

Understory insectivores are disproportionately affected

Throughout the Neotropics and North America, the impacts of extensive habitat loss, fragmentation, and degradation on avian communities have been well studied (Terborgh et al 1990, Şekercioğlu et al 2002, Ferraz et al 2007, Johnson 2007, Stouffer et al 2011, Bregman et al 2015, Visco et al 2015). Generally, fragmentation and its consequences are known to be more severe in tropical regions than in temperate ones (Şekercioğlu et al 2002, Sodhi et al 2011). For example, almost 80% of all threatened bird species are found in lowland and montane forests of the tropics (Sodhi et al 2011). Within tropical bird communities, rainforest dependent species which are often sedentary, interior-dwelling, highly specialised, have large home ranges, lower mobility, or are naturally rare, have been shown to be particularly vulnerable to fragmentation (Warburton 1997, Ford et al 2001, Moloney 2005, Ewers & Didham 2006, Korfanta et al 2012, Newbold et al 2014, Visco et al 2015). Similarly, species with specific life history traits including large body size, long generation time, low breeding success, or low clutch size are also more vulnerable. Foraging guilds are differentially affected by habitat fragmentation as well (Ewers & Didham 2006). Among forest-dependent birds, frugivores, nectarivores, and insectivores, are particularly vulnerable to habitat changes (Ford et al 2001, Şekercioğlu et al 2002, Moloney 2005, Newbold et al 2014). And of those guilds, insectivorous species are disproportionately impacted due to high habitat specificity, low mobility, and greater reliance on the forest

interior (Şekercioğlu et al 2002, Moloney 2005). As a consequence populations are declining globally, and the functional composition of forest communities are changing (Hausmann 2004, Peter et al 2015, Visco et al 2015). While much is known about the consequences of this (Bierregaard & Lovejoy 1989, Laurance et al 2002, Hausmann 2004, Stouffer et al 2011, Newbold et al 2014, Bennett et al 2015, Freeman et al 2015, Peter et al 2015, Kutt et al 2016), species level impacts are poorly understood. As managing and responding to the threat of habitat loss and degradation becomes imperative in the face of climate change and escalating biodiversity loss, it is widely acknowledged that detailed analysis of species-specific responses will be key (Ewers & Didham 2006, dos Anjos et al 2015, Hammond et al 2015, Hau & Goymann 2015).

There are fragmentation winners and losers

However, habitat fragmentation is not negative for all species. Several empirical studies have shown that some species adapt well to, or even benefit from, changed conditions e.g. species that have flexible behavioural repertoires, are more fecund, naturally more abundant, highly mobile, cooperative breeders, or superior competitors (Warburton 1997, Bender et al 1998, Matter 2000, Ford et al 2001, Laurance et al 2002, Fahrig 2003, González-Varo et al 2008, Maas et al 2009, Boscolo & Metzger 2011, Sodhi et al 2011, Bennett et al 2015). For example, the Noisy Miner (*Manorina melanocephala*) has been found to competitively exclude other species and increase differentially in smaller remnants, contributing to the declines of small-bodied birds throughout its expanding range (Briggs et al 2007, Bennett et al 2015). Similarly, an increased abundance of Chestnut-backed antbirds (*Myrmeciza exsul*) in fragments was suggested to be due to either fragments providing refuge from nest predation, or reduced niche overlap following release from competitors that rapidly disappeared from fragments (Visco & Sherry 2015). Third, the Thrushlike antpitta (*Myrmothera campanisona*), a species associated with tree-falls and other disturbance, was found to be able to colonise

forest fragments <100 ha after their isolation (Stratford & Stouffer 2013, Powell et al 2015). Lastly, breeding density of the Eurasian nuthatch (*Sitta europaea*) was found to be higher in more isolated woods. The authors attributed this to a combination of lower juvenile dispersal and lower predator density in smaller more isolated patches (González-Varo et al 2008). Though there may still be negative repercussions for ecosystems and communities, these cases are contrary to the general consensus that the effects of habitat fragmentation on populations and individuals are universally negative (Bender et al 1998, Matter 2000, Boscolo & Metzger 2011). Given that there is evidence for anomalies such as these, we must consider equally the potential for habitat fragmentation to produce both winners and losers and so examine what this might mean for communities and ecosystems (Ewers & Didham 2006, Bennett et al 2015).

Pale-yellow Robins persist in a fragmented landscape

The Pale-yellow Robin (PYR) *Tregellasia capito* is a territorial, understory insectivore known to inhabit both continuous forest and small fragments where other species no longer persist (Laurance et al 1996, Higgins & Peter 2002, Hausmann 2004, Moloney 2005, Freeman et al 2008, Laurance et al 2013). Sedentary in its range, two distinct populations are found on the east coast of Australia: one in south-east Queensland–northern New South Wales (ssp. *capito*); and, the second in Queensland's Wet Tropics (ssp. *nana*) (Higgins & Peter 2002). Listed as Least Concern by the IUCN Red List (BirdLife International 2016), total population size is unknown, but is suspected to be in decline due to clearing for agriculture (BirdLife Australia 2016, BirdLife International 2016). PYRs have been documented utilising a simple-pair or cooperative breeding strategy, and are commonly observed using both forest edges and interiors (pers. obs., Boles 1988, Laurance et al 1996, Higgins & Peter 2002, Laurance et al 2013). Beyond this, the ecology of PYRs is poorly documented, and their vulnerability to the impacts of habitat loss and fragmentation is largely unknown (Boles 1988, Male 2000, Higgins

& Peter 2002, BirdLife International 2016). A review of the literature did not provide evidence of either sensitivity or resilience to fragmentation. However, an unpublished study of patch size effects on the density of songbirds in rainforest remnants on the Atherton Tablelands found PYR populations were not reduced or absent from forest fragments, but that population density actually increased as patch size decreased (Adkins et al 2005). Similarly, a survey of bird communities on the Atherton Tablelands recorded the highest abundance of PYRs in the smallest fragments (Freeman et al 2008). This preliminary evidence suggested further study of a species that should be highly sensitive to fragmentation, yet appeared to persist in a fragmented landscape, was warranted.

Post-fragmentation persistence

In a review of the literature on the factors influencing the persistence of understory birds in tropical rainforest fragments, I investigated the relative effects of extrinsic patch-related (i.e. changes in patch size, isolation, and habitat quality), and intrinsic biological factors (population density, reproductive strategy, and competitive ability). The literature consistently concluded that rainforest dependent species are highly susceptible to extrinsic habitat fragmentation effects, and that populations restricted to small patches are much more likely to go extinct (Connor et al 2000, Ford et al 2001, Ewers & Didham 2006, Ferraz et al 2007, Şekercioğlu 2007, Korfanta et al 2012). When considering the ability of PYRs to persist in fragments where other species are lost, the literature led me to develop two principal hypotheses. First, habitat fragmentation, while not immediately detrimental to PYRs, may become problematic in the long term due to the effects of post-fragmentation crowding (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015) (Fig. 0.1).

Second, habitat fragmentation does not have a negative impact on the species owing to certain species-specific traits that confer protective or competitive

advantages, for example: cooperative breeding (Cooper 2000, Male 2000, Koenig & Dickinson 2004, Stevens et al 2015, Husemann et al 2015, Langmore et al 2016); habitat specialisation (Stouffer & Bierregaard 1995, Ford et al 2001, Ewers & Didham 2006); and, competitive exclusion (Diamond 1973, Ewers & Didham 2006, Stevens et al 2015, Bennett et al 2015, Kutt et al 2016). While I suspected that PYRs might be anomalous in some way, the weight of evidence in the literature, suggested that the first of these hypotheses should be most likely in the case of this small understory insectivore. Thus, the aim of my project was to test these hypotheses and determine if the PYR was a fragmentation loser, or winner.

Thesis overview

The key aim of my research project was to provide insights into the detailed dynamics of species-specific responses to post-fragmentation patch size, isolation, and habitat quality, and ultimately contribute to our understanding of how understory insectivore populations in the Wet Tropics are impacted by habitat loss and fragmentation. To this end, I designed and undertook empirical research to test two principle hypotheses and determine if the PYR is a habitat fragmentation winner or loser. Testing of these hypotheses are detailed in two data chapters. In Chapter 1, I present the first of my empirical results on PYR population densities, territory characteristics, and behavior, in relation to testing the hypothesis that PYR populations are experiencing post-fragmentation crowding, and subsequent density-related impacts. In contradiction to predictions based on the literature, I conclude that my results do not support the hypothesis, and that PYRs are likely indifferent to the effects of habitat fragmentation. As a consequence, the direction of my research changed and, in Chapter 2, I detail my findings regarding the alternative hypothesis that PYRs may be fragmentation 'winners' or, at the very least, fragmentation 'indifferent'. In this Chapter, I conclude that PYRs are a disturbed habitat specialist and, as such, benefit from the disturbance and degradation associated with fragmentation. Thus, I present a new non-sensitive

species model for understanding the effects of habitat fragmentation and avian community composition changes over time. Next, I discuss my results in the context of the current literature, and how they contribute to our current knowledge of how habitat loss and fragmentation impact PYR populations. I then relate this specifically to PYR population management, and present two potential management applications for my findings. Limitations of the project and opportunities for future research that build upon my findings are then identified and discussed. Finally, I draw conclusions about how habitat specialisation and cooperative breeding facilitates PYR persistence in fragments where other species are lost, and provide evidence that challenges the current paradigm that habitat fragmentation is universally negative for understory insectivores.

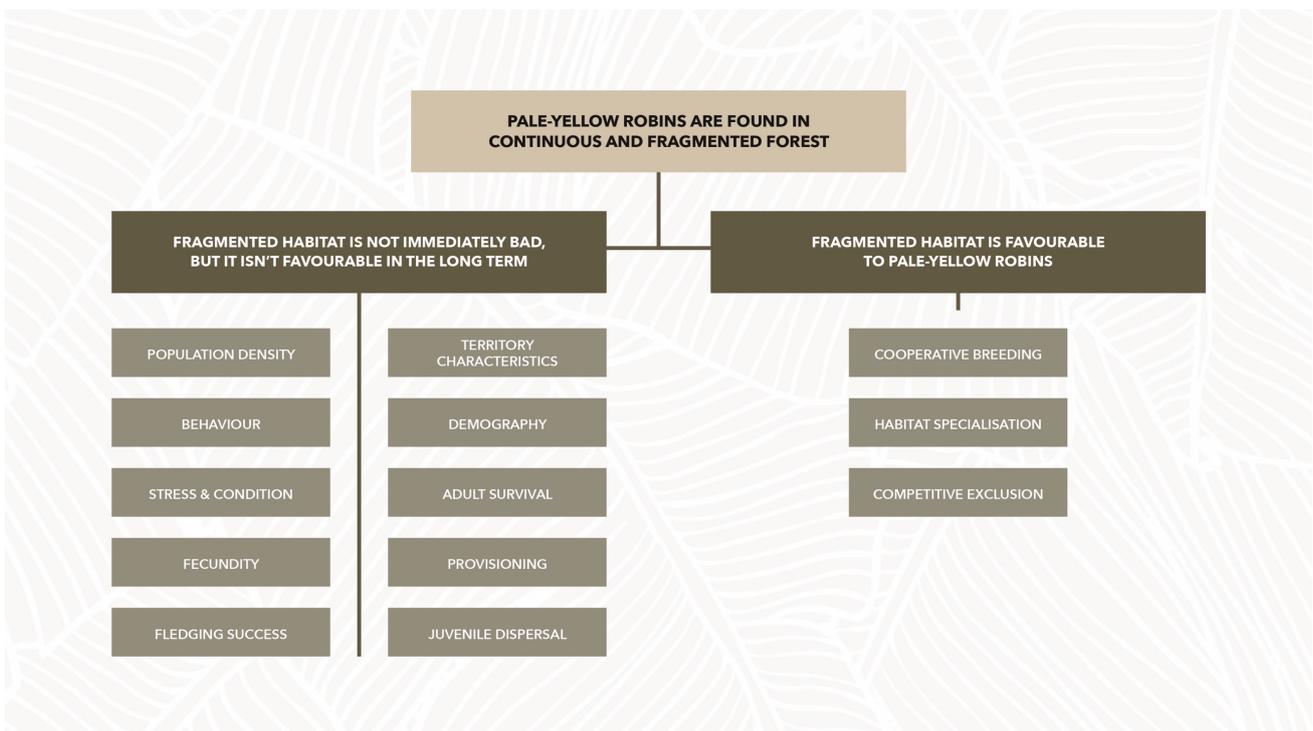


Figure 0.1: Pale-yellow Robins are known to persist in small fragments where other species have been lost (Warburton 1997, Higgins & Peter 2002, Hausmann 2004, Moloney 2005, Freeman et al 2008, Laurance et al 2013, Freeman et al 2015). The literature suggests there are two primary hypotheses. First, habitat fragmentation, while not immediately detrimental to PYRs, may become problematic in the long term due to the effects of post-fragmentation crowding (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). Second, habitat fragmentation does not have a negative impact on the species owing to species-specific traits that confer protective or competitive advantages, for example: cooperative breeding (Cooper 2000, Male 2000, Koenig & Dickinson 2004, Stevens et al 2015, Husemann et al 2015, Langmore et al 2016); habitat specialisation (Stouffer & Bierregaard 1995, Ford et al 2001, Ewers & Didham 2006); and, competitive exclusion (Diamond 1973, Ewers & Didham 2006, Stevens et al 2015, Bennett et al 2015, Kutt et al 2016).

CHAPTER 1

THE PALE-YELLOW ROBIN (*Tregellasia capito*) – A TROPICAL RAINFOREST UNDERSTORY INSECTIVORE INDIFFERENT TO HABITAT FRAGMENTATION

ABSTRACT

Habitat fragmentation is a key driver of biodiversity loss in forest ecosystems. Understory insectivores are especially at risk, and are being disproportionately lost from rainforest communities globally. This is because they disperse little, avoid edges, gaps and open habitats, and rarely use the matrix. Changes in community composition negatively impact trophic interactions and ecological processes. As biodiversity loss escalates, analysis of species-specific responses will be key to developing successful management and conservation strategies. The Pale-yellow Robin (PYR) *Tregellasia capito* is a territorial, understory insectivore known to inhabit continuous forest and small fragments where other species have been lost. According to the literature, habitat fragmentation, while not immediately detrimental, may become problematic in the long term due to the effects of post-fragmentation crowding. To test this, PYR populations in 16 complex notophyll vine forest sites on the Atherton Tablelands were studied (four fragment-size classes, each with four sites: >501 ha, >51 ha to 500 ha, 26–50 ha). ≥16 territories were surveyed in each class ($n = \geq 64$). To detect post-fragmentation crowding, PYR breeding territories were mapped and data was collected on territory defence behaviour. Comparisons were made between fragment-size classes to detect differences in PYR population densities, territory characteristics, and behaviour, resulting from a reduction in fragment size. I predicted PYR population densities would increase as overall fragment size decreased. Also that I would detect

density-related impacts on territory characteristics (i.e. reduced territory size, increased irregularity in shape, and decreased inter-territory distances), and PYR territory defence behaviour (i.e. reduced response time, increased number of defenders and rate of vocalisation). Contrary to these predictions, no evidence of post-fragmentation crowding was found. PYR densities, territory characteristics, and behaviour were remarkably consistent throughout all fragment-size classes. It was concluded PYRs on the Atherton Tablelands are not experiencing crowding or the associated density-dependent impacts other species experience post-fragmentation. Instead they appear to be indifferent to habitat fragmentation.

INTRODUCTION

Background

Habitat fragmentation is a key driver of biodiversity loss in forest ecosystems (Bender et al 1998, Fahrig 2003, Newbold et al 2014, Bregman et al 2015), with its consequences generally found to be more severe in tropical regions than in temperate ones (Şekercioğlu et al 2002, Sodhi et al 2011). Further to this, understory insectivores are especially sensitive to fragmentation and are being lost disproportionately from rainforest communities globally. This is because they disperse little, avoid edges, gaps and open habitats, and rarely use the deforested matrix surrounding the fragments (Stouffer & Bierregaard 1995, Warburton 1997, Şekercioğlu et al 2002, Moloney 2005, Şekercioğlu 2007, Sodhi et al 2011, dos Anjos et al 2015, Visco & Sherry 2015). The resulting changes in community composition have been shown to negatively interfere with trophic interactions and wider ecological processes (Zanette 2000, Hausmann 2004, Şekercioğlu 2007, Bregman et al 2015, Peter et al 2015, Powell et al 2015).

In Australia, Queensland's Wet Tropics region experienced extensive habitat loss and fragmentation throughout the 20th Century. Like other tropical regions around the globe, its avian populations are now at risk of decline and, in some cases, extinction due to various threats including continued clearing for housing and agriculture, and disturbance caused by logging (Moloney 2005, Birdlife Australia 2016, Evans & Evans 2017). As responding to the threat of habitat loss and fragmentation becomes imperative in the face of escalating biodiversity loss, it is widely acknowledged that detailed analysis of species-specific responses will be key to developing successful future management and conservation strategies (Ford et al 2001, Sodhi et al 2011, Hammond et al 2015, Hau & Goymann 2015).

Pale-yellow Robins

The Pale-yellow Robin (PYR) *Tregellasia capito* is a territorial rainforest understory insectivore distributed in two separate locations along the east coast of Australia. Sedentary in its range, the northernmost subspecies (*Tc nana*) is found in both continuous rainforest and fragments throughout Queensland's Wet Tropics. It is known to utilise both forest edges and interiors, and to persist in small fragments where other species have been lost (Warburton 1997, Higgins & Peter 2002, Hausmann 2004, Moloney 2005, Freeman et al 2008, Laurance et al 2013, Freeman et al 2015). Total population size is unknown but suspected to be in decline. Beyond this, the ecology of the species is poorly documented (Male 2000, Higgins & Peter 2002, BirdLife International 2016).

When considering this species' ability to persist in fragments where others do not, a review of the literature led me to develop two principal hypotheses. First, habitat fragmentation, while not immediately detrimental to PYRs, may become problematic in the long term due to the effects of post-fragmentation crowding (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015) (Fig. 0.1). Second, habitat fragmentation does not have a negative impact on the species owing to certain species-specific traits that confer protective or competitive advantages, for example: cooperative breeding (Cooper 2000, Male 2000, Koenig & Dickinson 2004, Stevens et al 2015, Husemann et al 2015, Langmore et al 2016); habitat specialisation (Stouffer & Bierregaard 1995, Ford et al 2001, Ewers & Didham 2006); and, competitive exclusion (Diamond 1973, Ewers & Didham 2006, Stevens et al 2015, Bennett et al 2015, Kutt et al 2016) (Fig 0.1). The weight of evidence in the literature (as outlined below), suggests that the first of these hypotheses is most likely for this small understory insectivore. Therefore, the aim of my study was to test this hypothesis.

Post-fragmentation crowding

Understory insectivores avoid open areas and are surprisingly poor at dispersal, despite their obvious mobility (Zanette 2001, Şekercioğlu et al 2002, Laurance et al 2002, Hausmann 2004, Visco et al 2015). After habitat loss, population density and species richness often increase within remaining habitat, as displaced individuals attempt to resettle (Bierregaard & Lovejoy 1989, Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). After a period of relaxation that can take up to several decades, this crowding eventually gives way to long-term extinction debts (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). This process has been demonstrated in many bird species, where an increase in population density following fragmentation has been shown to negatively impact: territory characteristics, such as size, shape, and spatial arrangement (Zanette 2001, Wilkin et al 2006, Stouffer 2007, Viblanc et al 2014); behaviour (Yoon et al 2012); population demography (Wilkin et al 2006, Korfanta et al 2012, Stevens et al 2015); stress and body condition (Kitaysky et al 2003, Bonier et al 2009, Escribano-Avila et al 2013, Dettmer et al 2014, Homberger et al 2015, Newman et al 2015); adult survival (Korfanta et al 2012, Wilkin et al 2006); fecundity (Donovan & Lamberson 2001, Wilkin et al 2006, Fasce et al 2011, Hartmann et al 2017); provisioning (Moore & Class 2010); fledging success (Wilkin et al 2006, Fasce et al 2011, Lebeuf & Giroux 2014, Stevens et al 2015); and, juvenile dispersal (Zanette 2001, Ewers & Didham 2006, González-Varo et al 2008, Blackmore et al 2011, Wesolowski 2015). These indicators of fragmentation impacts are hierarchical and are listed above in the order changes that would most likely become detectable (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015, Visco et al 2015).

Early indicators

Post-fragmentation crowding alters intra- and inter-specific interactions through increased competition and other density-dependent processes (Zanette 2000,

Fasce et al 2011, Sodhi et al 2011). Territory size and regularity of territory shape may also be reduced in crowded conditions as less successful competitors 'fit in' around more successful ones (Cooper 2000, Zanette 2001, Wilkin et al 2006, Johnson 2007, Stouffer 2007, Hartmann et al 2017). The 'enemy-free' space between territories also decreases (Jeffries & Lawton 1984, Adkins et al 2005, Lebeuf & Giroux 2014), resulting in more frequent, longer and intense aggressive interactions with conspecific neighbours (Brown 1964, Eason & Hannon 1994, Fasce et al 2011, Yoon et al 2012, Lebeuf & Giroux 2014, Bhardwaj et al 2015, Bregman et al 2015, Davies & Sewall 2016).

One significant impact of all these processes is an upregulation in secretion of the 'stress hormone' corticosterone (Creel et al 2013, Viblanc et al 2014, Newman et al 2015, Blondel et al 2016). In the short term, corticosterone has a positive effect on fitness. However, over extended periods, it can have serious negative impacts on individuals and populations (Kitaysky et al 2003, Dettmer et al 2014, Homberger et al 2015), as identified above.

Overview of chapter

The aim of this study was to test the hypothesis that habitat fragmentation results in crowding of PYRs within remaining habitat – a process that may have either current or future negative impacts on individuals and the long-term viability of populations. A secondary aim was to contribute sufficiently to our knowledge of PYR ecology in order to assess the species utility as a model for understanding the effects of habitat fragmentation on tropical rainforest understory birds in general. To this end, I quantified potential crowding in 16 rainforest sites on the Atherton Tablelands within four fragment-size classes. Data collection focused on the early indicators likely to exhibit post-fragmentation crowding effects i.e. population density, territory characteristics, and levels of aggressive territory defence behaviour (Ewers & Didham 2006). Predictions based on the existing literature suggested that I would

detect an increase in population density (increased groups and individuals per ha), changed territory characteristics (decreased size / increased diversity of shape / decreased inter-territory distances), and an increase in aggression during territory defence (shorter response time / more defenders / more vocalisation) as fragment size decreased.

METHODS

Study sites and sampling design

The study area was located near Millaa Millaa (17°30'39.1"S, 145°36'50.2"E) on the Atherton Tablelands, in Queensland's Wet Tropics. To determine if post-fragmentation crowding has occurred in rainforest remnants of different sizes, I identified four rainforest sites in each of four fragment-size classes: continuous rainforest (>501 ha) acting as reference for normal conditions, large remnants (>51 ha to 500 ha), medium remnants (26–50 ha), and small remnants (<25 ha), giving a total of 16 study sites (Appendix A: *Schedule of study sites*, Appendix B: *Study sites map*). I then aimed to study the characteristics of at least 16 PYR territories in each fragment-size class (≥ 4 territories in each of the 16 sites, $n = \geq 64$) in a nested design. All sites were above 700 m ASL and classified as vegetation Type 5a (Tracey & CSIRO 1982), or 'Regional Ecosystem 7.8.4a' (DEHP 2017). This ecosystem is described as 'complex notophyll vine forest' and is found only on basaltic krasnozems in a very limited area of the cloudy-wet rainfall zone of the Wet Tropics. Its biodiversity status is listed as 'Endangered' (DEHP 2017). To identify remnants and continuous areas of Regional Ecosystem 7.8.4a, I ran the Queensland Globe 'Biota' category globe (Business Queensland 2016) in Google Earth (Google 2016) and specified the layer: 'Regional Ecosystem (RE) mapping' > 'Biodiversity RE status version 9.0', 'Remnant (2013)' > 'Endangered – Dominant vegetation'.

Study sites were chosen based on their size, which I measured by copying the shape details from a 'RE7.8.4a.kmz' layer file (Google 2016) and pasting the details into the Earth Point KML Shapes online calculator (Clark 2016). Sites were located on a mix of private land and protected areas, with land tenure for each site having been determined by displaying the 'Land Parcel Tenures' layer in Queensland Globe (Business Queensland 2016). The vegetation at most of the sites was quite dense and difficult to move through. Most of the remnants were located around valleys and natural watercourses, and it was apparent that the reason many were left un-cleared was because machinery could not access the very steep terrain.

Field kit

Due to the highly mobile nature of the fieldwork, a wearable field kit with light and compact equipment was used. It included a Garmin Forerunner[®] 220 watch for recording the time and tracking my movement (Appendix C: *Garmin Forerunner[®] 220 survey area tracking*), a Garmin Connect[™] iPhone app (Garmin Australasia 2016) for syncing and visualising Garmin Forerunner[®] 220 data, the iOS Maps app (Apple 2017) for orientating myself within the forest, a Garmin Oregon[®] 600 handheld GPS for recording waypoints and navigation, the Pizzey & Knight Birds of Australia Digital Edition iPhone app (Gibbon Multimedia Australia 2016) for bird identification and PYR call recordings, an iPhone 6 and Ultimate Ears UE BOOM 2 waterproof Bluetooth speaker for playback of PYR calls, binoculars, pen, notebook, and secateurs. Due to the high power requirements of the field kit, a PTG Powerbank Reserve High Capacity 5200mAh charger was used to charge devices on-the-go, as required.

Territory mapping

Typically, a transect-based spot mapping technique is employed to map bird territories (Terborgh et al 1990, Bibby et al 2000, Shankar Raman 2003, Stouffer

2007, Boscolo & Metzger 2011, Davies & Sewall 2016). However, this method would not produce the level of detail required to test my hypothesis. Given this, I developed a high-resolution mapping technique using playback of PYR calls that capitalised on the territorial nature of the species (Fig. 1.1). Upon entry into a site, a tracking session was begun on the Garmin Forerunner[®] 220 watch so that the survey area could be estimated at a later stage. The first potential PYR territory was located by walking around and playing standardised recordings of PYR calls on an iPhone 6 connected to the UE BOOM 2 Bluetooth speaker at an approximated natural volume of 75–85 dB at 1 m (Davies & Sewall 2016) to elicit a territorial defence response (hereafter referred to as 'playback').

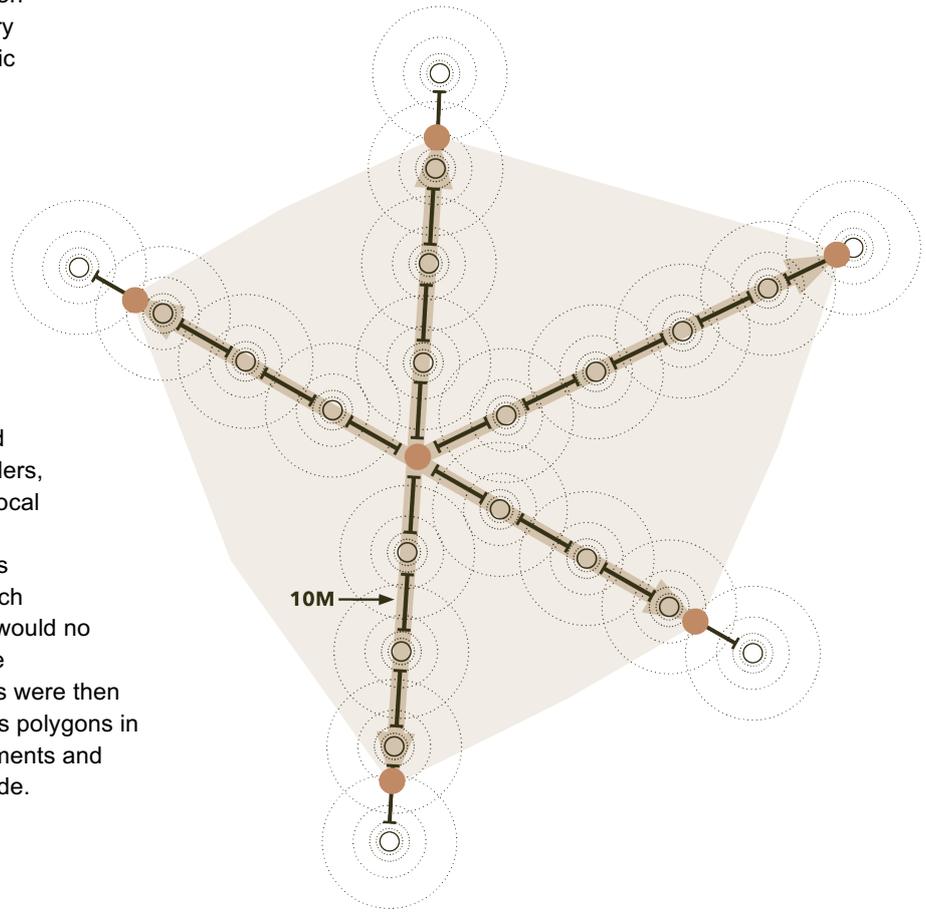
Once an individual or group of birds was located, an 'initial' waypoint was marked. I then moved away from the initial waypoint in a straight line in a randomly chosen direction stopping approximately every 10 m (depending on responsiveness of the territory defender/s, terrain, or vegetation density) and repeated the playback. At each playback point, the time of commencement of playback (± 1 s) was called to a field assistant who remained at the previous playback point. The assistant then confirmed when the bird/s moved from their last known position towards me at the new playback point. When the defender/s were visually identified as having moved to within 5 m of the new playback point, territory defence behaviour including the number of defenders, time of re-detection, and if they were vocal or not was noted. This was repeated in the same direction until the defender/s were no longer detectable, or were unwilling to move to the next playback point within 10 minutes. The last point at which the birds were observed was then marked as the 'end' waypoint of that direction. I then returned to the initial waypoint and repeated the procedure in another direction approximately 72 degrees to the left or right of the last. This procedure was conducted at least five times for each territory.

Adjacent territories that were detected through boundary disputes, or vocal response to playback were noted and targeted for territory mapping at a later time.

This also facilitated measurement of inter-territory distances between clustered territories. Once mapping of a territory was completed, the next potential PYR territory was located by moving away in the direction of a previously detected territory, or by beginning the walk and playback process again in an area outside of known PYR territory boundaries. Upon completion of activity and exit from the site the Garmin Forerunner[®] 220 watch tracking session was concluded (Appendix C: *Garmin Forerunner[®] 220 survey area tracking*). As many territories as possible were mapped during each session – usually two or three per day – but up to a maximum of five on days where territories were adjacent and the birds were responsive to playback.

All data collection was carried out from October to December during the 2016 breeding season when the birds were expected to be most competitive and, therefore, responsive to intruders to their territory. Daily selection of which forest site/s to survey was random. On all but three days, the weather was warm and sunny. On the days when it rained, no significant difference in bird responsiveness to playback was discernible. However, data on territory defence behaviour was not captured on those days to ensure that the sound of the rain, or any reluctance to defend territories in poor weather did not confound the data. Most days birds appeared most active between 7:00am and 12:00pm, and again from 3:00pm to ~ 4:30pm, but surveying was not limited to these times as some groups were happy to defend their territory through the middle of the day. Of the available PYR recordings in the Pizzey & Knight Birds of Australia app, '*Typical sounds race nana. Cairns, QLD. Fred van Gessel*' was consistently most effective, followed by '*Typical sounds race nana. Murray Falls, Girramay NP, QLD. Fred van Gessel*' (Gibbon Multimedia Australia 2016). A 'no-bird' response to playback was decided after a maximum of two five-minute calling periods without detection of a response.

Figure 1.1: High-resolution Pale-yellow Robin territory mapping using conspecific playback. Each territory was located and an 'initial' waypoint was marked. From the initial waypoint, defenders were lured out in five different directions with playback every ~10 m. At each playback point, the time to respond (± 1 s), number of defenders, and whether they were vocal or not ('yes' / 'no') was recorded. A waypoint was marked at the 'end' of each direction when the birds would no longer engage in defence behaviour. The waypoints were then used to draw territories as polygons in ArcGIS so that measurements and calculations could be made.



Data analyses

Population density

To determine if a decrease in overall fragment size resulted in an increase in PYR densities as predicted, GPS waypoints and tracking data were visualised in ArcGIS (ESRI 2011) (Appendix D: *Data visualisation*). In order to calculate highly accurate population densities, I wanted to avoid extrapolating local area density data across whole fragment study sites. The Garmin Forerunner[®] 220 tracking data was key to doing this. The total survey area at each site was determined by drawing a polygon with an approximately 30 m buffer on either side of the Forerunner[®] 220 tracks. This buffer distance was based on several in-field assessments of playback audibility that ranged from 30 to 60 m. From this, the mean number of territories per ha of surveyed area (mapped and others detected but not mapped), and mean number of individuals per ha (determined as the maximum number of birds seen at

any one time in mapped territories), at each site was calculated. Statistical tests were then performed in S-Plus (TIBCO Software Inc. 2017). First, data was tested for normality and homogeneity of variance. An analysis of variance (ANOVA) was then performed to test for differences in group and individual densities between fragment-size classes.

Territory characteristics

To determine if the size, shape and spatial arrangement of PYR territories were affected by a decrease in overall fragment size, I worked again with the GPS waypoint data in ArcGIS (ESRI 2011). Each territory was drawn as a polygon by connecting the 'end' waypoints by a straight line. First, territory size was calculated as the area of the polygon (ha) by using the 'Calculate Geometry' function in the Attribute Table. The data was tested for normality and homogeneity of variance in S-Plus (TIBCO Software Inc. 2017). A Generalised Linear Mixed Model (GLMM) was then used to test for differences in territory size between fragment-size classes, with 'Site' as a random-effect grouping variable. In addition to this, I performed a linear regression on combined territory size data from all fragment-size classes ($n = 66$) to test if there was a relationship between population density and territory size.

Second, territory shape was determined by measuring the length (longest point-to-point) and width (shortest point-to-point) of each territory (± 1 m) in ArcGIS (ESRI 2011) and calculating a ratio value (width / length). This data was then arcsine transformed as appropriate for proportional data in statistical tests (Whitlock & Schluter 2009). The data were tested for normality and homogeneity of variance using S-Plus (TIBCO Software Inc. 2017). Again, a Generalised Linear Mixed Model (GLMM) was used to test for differences in shape between fragment-size classes, with 'Site' specified as a random-effect grouping variable.

Finally, the spatial arrangement of PYR territories was analysed. This was done by measuring the inter-territory distance between as many territory pairings as possible in ArcGIS (ESRI 2011), with a single direct boundary-to-boundary measure between the closest points of any two territories. Of 105 distances measured, 56 inter-territory distances were 0 m. Because of this, I undertook two analyses of spatial arrangement. First, I ran a chi-squared test in S-Plus (TIBCO Software Inc. 2017) to determine if the frequency of 0 m distances was higher than expected in any fragment-size class. Second, to determine if there was variation between fragment-size classes when the distance was greater than 0 m, all records of 0 m inter-territory distances were removed, and the remaining data tested for normality and homogeneity of variance. Data were Log transformed as appropriate. A Linear Mixed Effects Model (LMM) was then used to test whether mean inter-territory distance differed between fragment-size classes (R Core Team 2017, RStudio 2017). Again, I specified 'Site' as a random-effect grouping variable and tested for interactions between classes while allowing each one to have an independent distribution of residuals using the 'varIdent' function in the 'nlme' package (R-core R-core@R-project.org 2009).

Behaviour

To determine if a post-fragmentation crowding effect could be detected in the behaviour of PYRs, I analysed territorial defence data. This included response time ($n = 294$), number of defenders ($n = 294$), and proportion of vocal defence ($n = 294$). All data were tested for normality and analysis was adjusted accordingly. Response time was calculated as the number of seconds elapsed from the time of commencement of playback to the time of re-detection. I tested for differences between fragment-size classes using logistic regression via a Linear Mixed Effects Model (LMM) in RStudio (R Core Team 2017, RStudio 2017). Individual variance within each fragment-size class was accounted for by specifying the 'varIdent' function in the 'nlme' package (R-core R-core@R-project.org 2009). 'Site' was

specified as a random-effect grouping variable. Next, to test if the number of defenders in different fragment-size classes differed from what would be expected, I grouped the data into two categories (1 and >1 defenders) and ran a chi-squared test. Lastly, differences in the proportion of vocalisation ('yes' / 'no') during territory defence were tested in RStudio (R Core Team 2017, RStudio 2017). Response 'yes' was assigned as 1 and 'no' was assigned as 0. I used logistic regression via a Linear Mixed Effects Model (LMM) to test for differences between fragment-size classes. Individual variance within each fragment-size class was accounted for by specifying the 'varIdent' function in the 'nlme' package (R-core R-core@R-project.org 2009). 'Site' was specified as a random-effect grouping variable.

RESULTS

Population density

Post-fragmentation PYR densities do not exhibit any crowding effect.

The density of territories did not differ significantly between different fragment-size classes (Shapiro-Wilks: $W = 0.95$, $P = <0.0001$, Levene's: $F_{(3, 12)} = 1.22$, $P = 0.35$, ANOVA: $F_{(3, 12)} = 1.42$, $P = 0.28$), even though there was a tendency for some large fragments to have lower territory densities. On average, there is one PYR group / territory per two ha of forest surveyed (Fig. 1.2). Similarly, the density of individuals per ha does not change as fragment size reduces (Shapiro-Wilks: $W = 0.98$, $P = 0.92$, Levene's: $F_{(3, 12)} = 1.1$, $P = 0.39$, ANOVA: $F_{(3, 12)} = 1.46$, $P = 0.27$), with approximately two birds observed per two ha of forest surveyed across all fragment-size classes (Fig. 1.3).

Territory characteristics

PYR territory characteristics do not suggest that any crowding effect is present. First, territory size did not change as fragment size decreased (Shapiro-Wilks: $W = 0.97$, $P = 0.072$, Levene's: $F_{(3, 62)} = 1.3$, $P = 0.28$, GLMM: $F_{(3, 12)} = 2.23$, $P = 0.14$). PYR territories ($n = 66$) are consistently around 0.79 ha ($SD \pm 0.34$) across all fragment-size classes (Fig. 1.4). Linear regression also shows there is no overall relationship between territory density and territory size ($n = 66$) ($F_{(1, 64)} = 0.0026$, $R^2 = 0.00004$, $P = 0.96$) (Fig. 1.5), or density of individuals and territory size ($n = 66$) ($F_{(1, 64)} = 3.11$, $R^2 = 0.046$, $P = 0.083$) (Fig. 1.6).

Second, territory shape did not vary within or between fragments of different sizes (Shapiro-Wilks: $W = 0.98$, $P = 0.39$, Levene's: $F_{(3, 62)} = 1.45$, $P = 0.24$, GLMM: $F_{(3, 12)} = 1.28$, $P = 0.33$). Territories are consistently around 1.7 times as long as they are wide across all fragment-size classes (Fig. 1.7).

Finally, the distances between territories did not vary as fragment size decreased. The frequency of 0 m inter-territory distances was not greater than would be expected in any fragment-size class ($\chi^2 = 6.17$, $df = 3$, $P = 0.1$) (Fig. 1.8). Where inter-territory distances were greater than 0 m, there was also no significant difference in mean inter-territory distance between fragment-size classes (LMM: $F_{(3, 10)} = 1.76$, $P = 0.22$). There was however, a tendency for there to be greater variation in inter-territory distances in large fragments, indicating that large distances occurred more often in this fragment-size class than in continuous forest, medium, or small fragments (Fig. 1.9).

Behaviour

PYR territory defence behaviour did not indicate a post-fragmentation crowding effect. There was no significant difference in response time between individuals from different fragment-size classes (LMM: $F_{(3, 6)} = 0.91$, $P = 0.5$). Mean response time was 66 seconds (SD \pm 82) in small fragments ($n = 54$), 113 seconds (SD \pm 127) in medium fragments ($n = 87$), 97 seconds (SD \pm 103) in large fragments ($n = 81$), and 146 seconds (SD \pm 136) in continuous forest ($n = 72$) (Fig. 1.10).

The number of territory defenders did differ significantly between fragments of different sizes however, but not in the way expected if a post-fragmentation crowding effect was present (i.e. increasing number of defenders as patch size decreased). Instead, investment in territory defence was actually lower in large fragments than in any other fragment-size class, where more often territory defence was undertaken by a single bird ($\chi^2 = 10.54$, $df = 3$, $P = 0.015$). In other classes, territory defence by a single bird, or more than one bird, were just as likely (Fig. 1.11).

The proportion of times birds were vocal when defending their territory did not differ significantly between fragment-size classes (LMM: $F_{(3, 6)} = 0.69$, $P = 0.59$). There was a tendency, however, for birds in large fragments to be vocal more of the time. On average, defending birds were vocal 40% (SD \pm 34) of the time across all classes. Mean small 49% (SD \pm 38) ($n = 4$), medium 37% (SD \pm 40) ($n = 10$), large 64% (SD \pm 19) ($n = 4$), and continuous 27% (SD \pm 23) ($n = 6$) (Fig. 1.12).

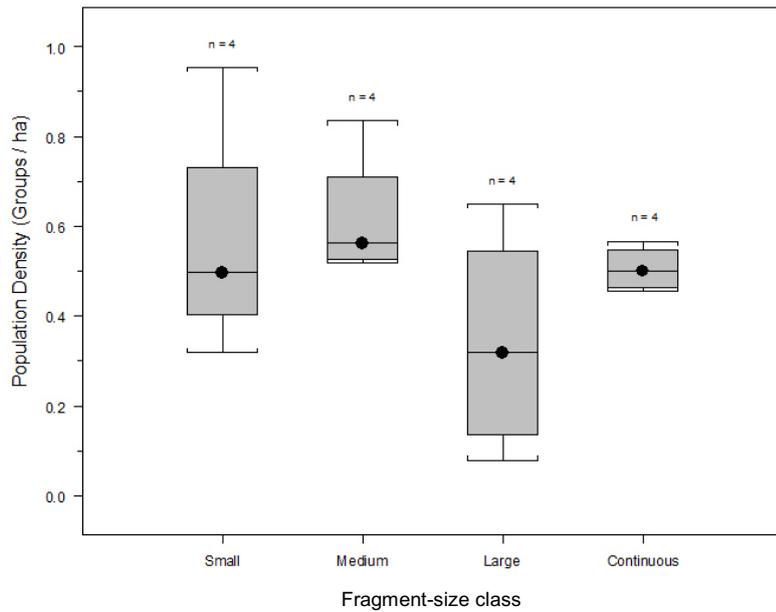


Figure 1.2: Density of PYR groups across 16 rainforest study sites in four fragment-size classes. Post-fragmentation PYR densities do not exhibit a post-fragmentation crowding effect (ANOVA: $P = 0.28$). On average there is one group of PYRs per two ha of forest surveyed. There is a tendency for some large fragments to have lower territory densities. Population densities in continuous forest are very consistent. Mean: small 0.57 (SD ± 0.27) ($n = 4$), medium 0.62 (SD ± 0.15) ($n = 4$), large 0.34 (SD ± 0.26) ($n = 4$), continuous 0.51 (SD ± 0.06) ($n = 4$).

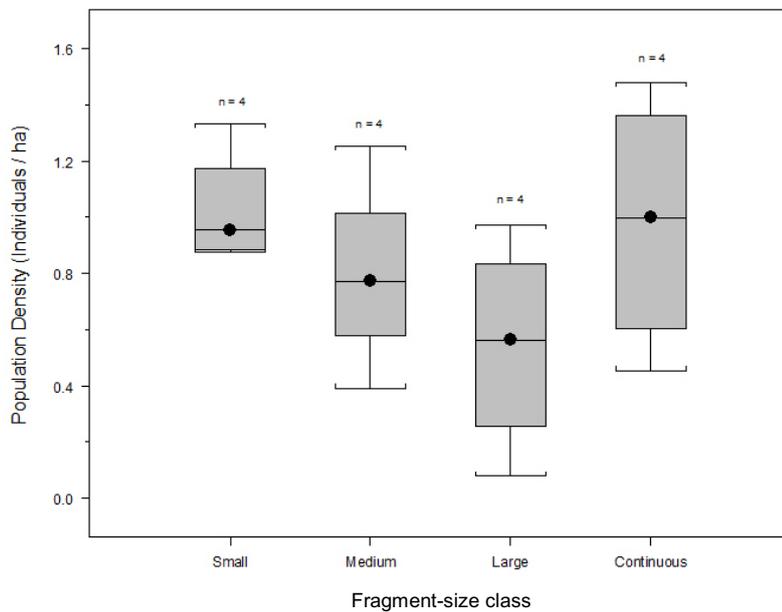


Figure 1.3: Density of PYR individuals across 16 rainforest study sites in four fragment-size classes. The density of individuals per ha does not change as fragment-size class reduces (ANOVA: $P = 0.27$). On average there are two PYRs per two ha of forest surveyed. There is a tendency for decreasing density of individuals as fragment size increases. Mean: small 1.03 (SD ± 0.21) ($n = 4$), medium 0.80 (SD ± 0.35) ($n = 4$), large 0.55 (SD ± 0.38) ($n = 4$), continuous 0.98 (SD ± 0.47) ($n = 4$).

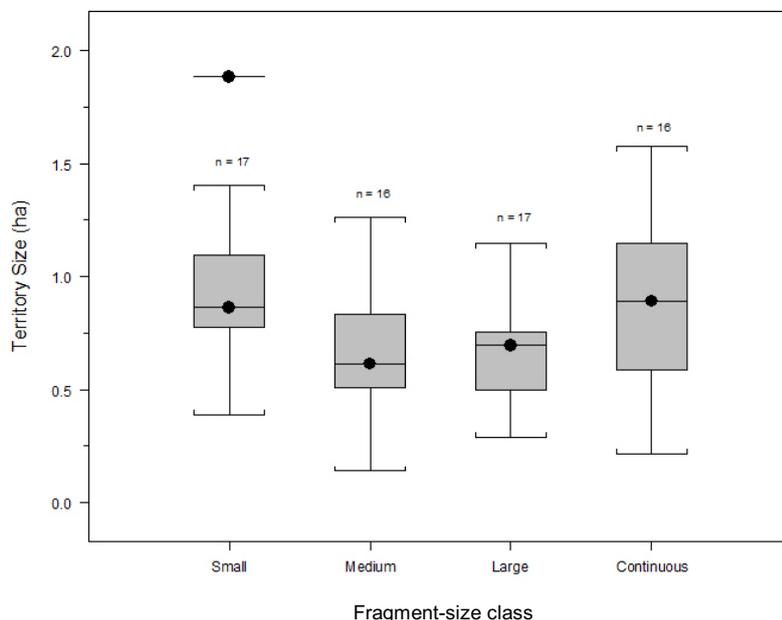


Figure 1.4: Size of PYR territories in 16 sites in four fragment-size classes. Calculated as the area of a polygon drawn in ArcGIS using GPS waypoints taken during territory mapping activities. Territory size does not indicate post-fragmentation crowding effects (GLMM: $P = 0.14$). Territories ($n = 66$) are consistently around 0.79 ha (SD ± 0.34) across all fragment-size classes. Mean: small 0.93 ha (SD ± 0.35) ($n = 17$), medium 0.68 (SD ± 0.29) ($n = 16$), large 0.64 (SD ± 0.23) ($n = 17$), continuous 0.89 (SD ± 0.38) ($n = 16$).

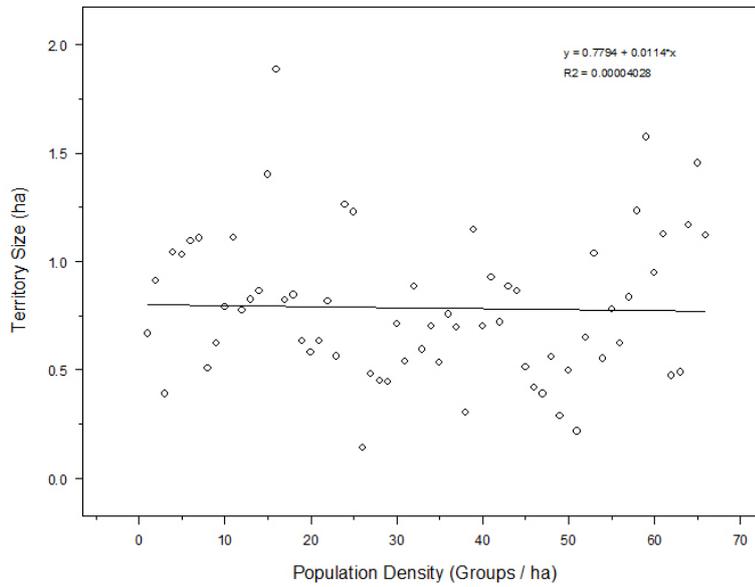


Figure 1.5: Linear regression shows there is no relationship between density of PYR groups and PYR territory size ($R^2 = 0.00004$, $P = 0.96$) ($n = 66$).

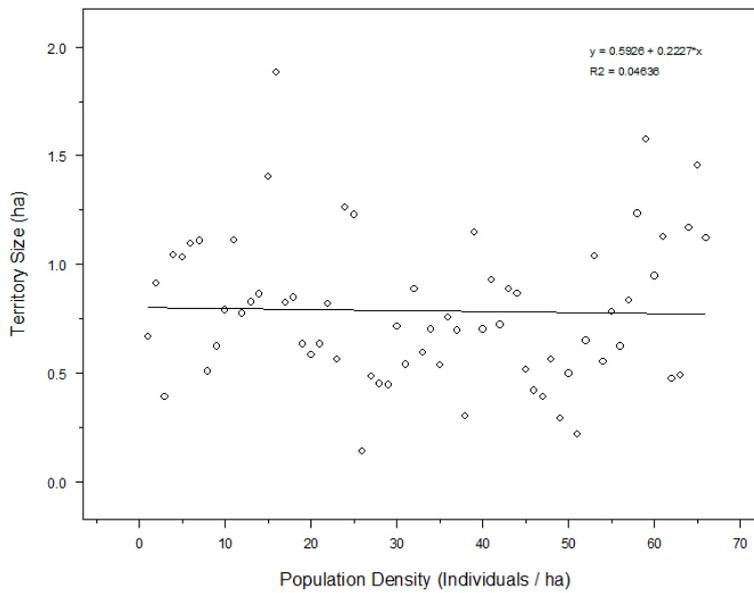


Figure 1.6: Linear regression shows there is no relationship between density of PYR individuals and PYR territory size ($R^2 = 0.046$, $P = 0.083$) ($n = 66$).

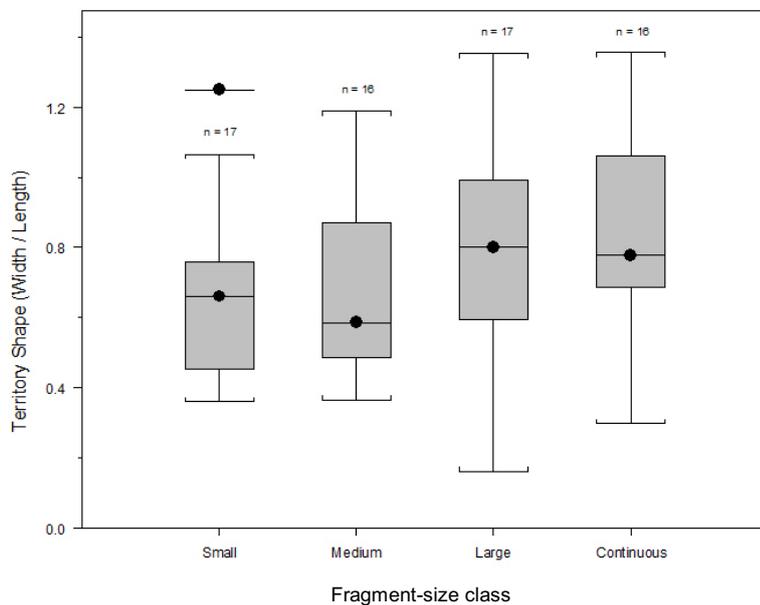


Figure 1.7: Territory shape measured as the length (longest point-to-point) and width (shortest point-to-point) of each territory (± 1 m), calculated as a ratio (W / L) and arcsine transformed for analysis. The shape of PYR territories in 16 sites in four fragment-size classes does not indicate post-fragmentation crowding effects (GLMM: $P = 0.33$). Territories ($n = 66$) are consistently around 1.7 times as long as they are wide across all fragment-size classes. Mean: 126 x 78 m.

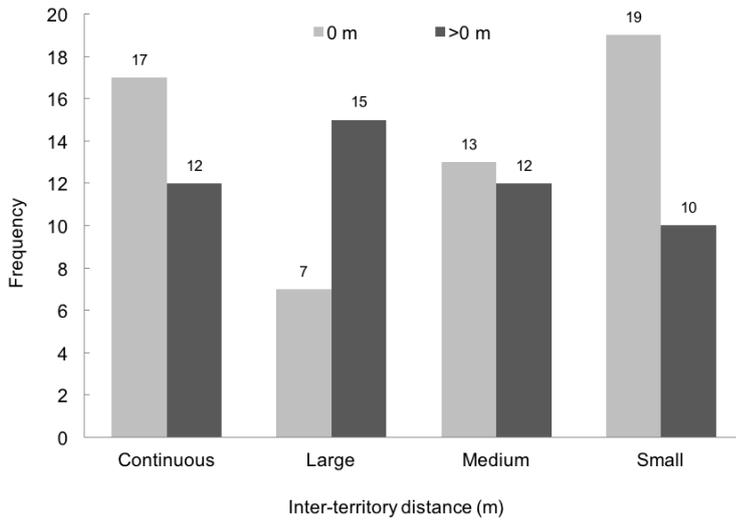


Figure 1.8: Frequency of 0 m and >0 m distances between PYR territories. Distances measured as a single direct boundary-to-boundary measure between the closest points of any two territories ($n = 105$). The frequency of 0 m inter-territory distances was not greater than would be expected in any fragment-size class ($\chi^2 = 6.17$, $df = 3$, $P = 0.1$). There is however, a tendency for more 0 m distances in small fragments, and more >0 m distances in large fragments.

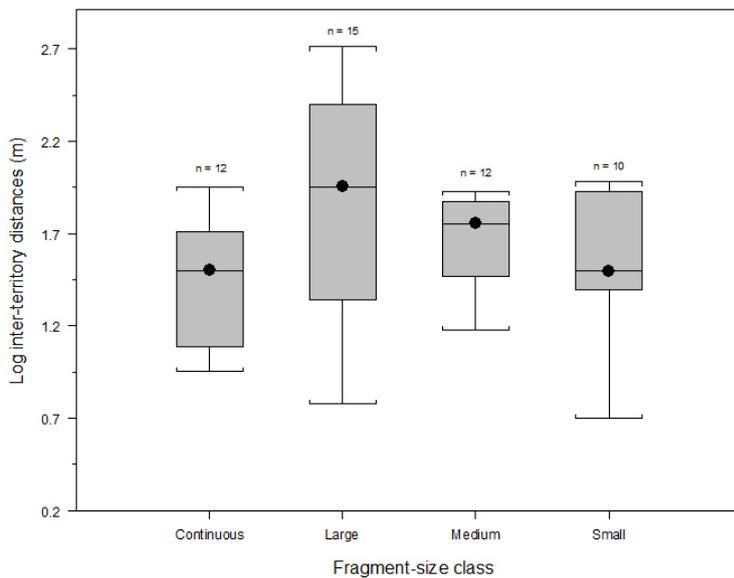


Figure 1.9: Distances between PYR territories greater than 0 m ($n = 49$). There was no difference in mean inter-territory distance between fragment-size classes (LMM: $P = 0.22$). Significantly greater variation in inter-territory distances in large fragments (Levene's: $P = 0.029$) were accounted for using the varIdent function in the 'nlme' package (R-core R-core@R-project.org 2009). Mean: small 43.70 m (SD \pm 34.77) ($n = 10$), medium 52.58 m (SD \pm 23.45) ($n = 12$), large 136.07 m (SD \pm 150.48) ($n = 15$), continuous 37.08 m (SD \pm 25.91) ($n = 12$).

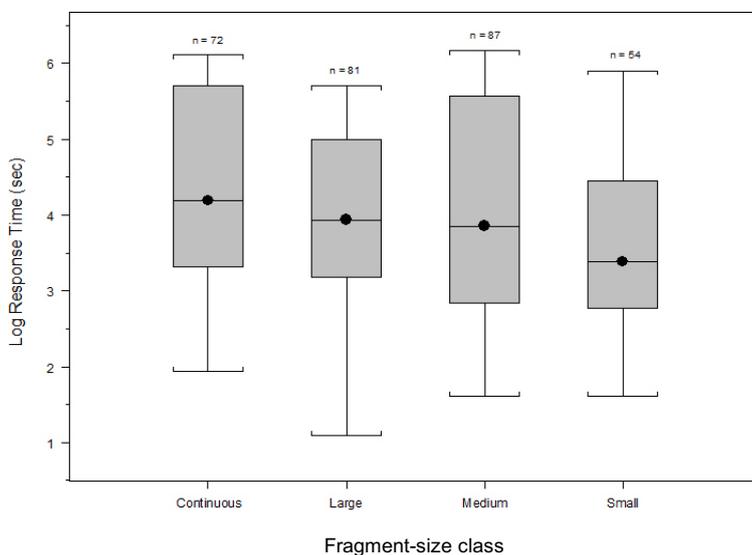


Figure 1.10: PYR territorial defence response time to playback in 16 sites in four fragment-size classes ($n = 294$). There was no significant difference in response time between individuals from different fragment-size classes (LMM: $P = 0.49$). Mean response time: small 66 seconds (SD \pm 82) ($n = 54$), medium 113 seconds (SD \pm 127) ($n = 87$), large 97 seconds (SD \pm 103) ($n = 81$), continuous 146 seconds (SD \pm 136) ($n = 72$).

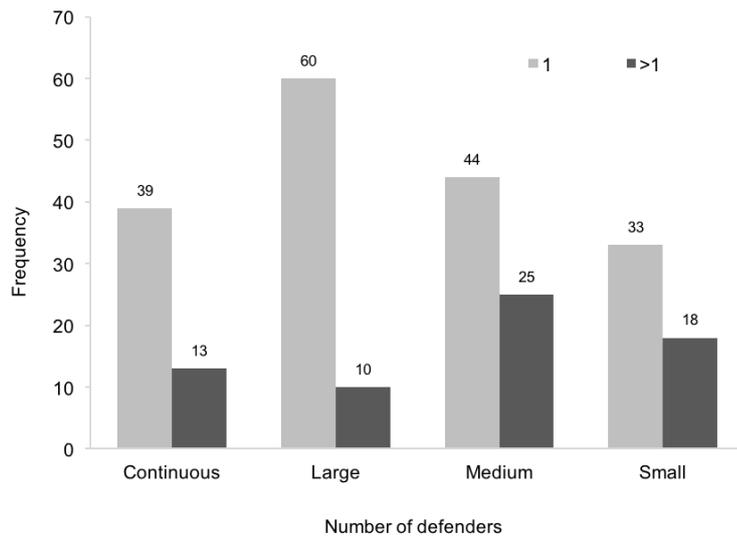


Figure 1.11: Frequency of 1 bird and >1 birds undertaking territory defence between PYR territories, measured as the number of defenders recorded at each call point ($n = 244$). The observation of just 1 defender was greater than would be expected in the large fragment-size class ($\chi^2 = 10.54$, $df = 3$, $P = 0.015$). In other classes, territory defence by a single bird, or more than one bird, were just as likely.

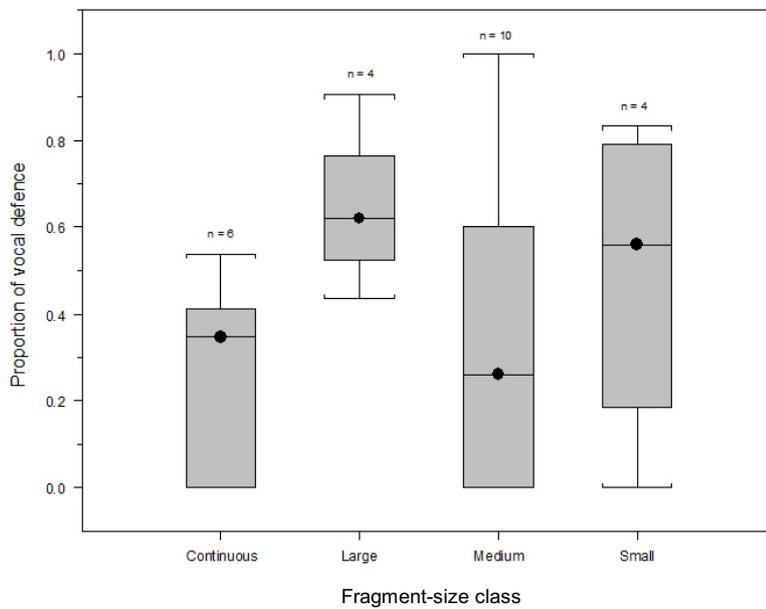


Figure 1.12: Proportion of times PYRs were vocal during territory defence. There was no difference in rate of vocalisation between fragment-size classes (LMM: $P = 0.69$). Unequal variance within fragment-size classes was accounted for using the varIdent function in the 'nlme' package (R-core R-core@R-project.org 2009). On average, defending birds were vocal 40% (SD ± 34) of the time across all classes. Mean small 49% (SD ± 38) ($n = 4$), medium 37% (SD ± 40) ($n = 10$), large 64% (SD ± 19) ($n = 4$), continuous 27% (SD ± 23) ($n = 6$).

DISCUSSION

The primary aim of this study was to determine if PYR populations on the Atherton Tablelands of Queensland's Wet Tropics are experiencing the negative effects of post-fragmentation crowding within remaining rainforest remnants. While PYRs persist in fragments of all sizes throughout their range (Male 2000, Higgins & Peter 2002) several decades after deforestation within the Atherton Tablelands (Kanowski et al 2003, Evans & Evans 2017), the long-term viability of these populations is unknown. The literature, however, suggests a high susceptibility of small rainforest understory insectivores like the PYR to the negative impacts of habitat fragmentation (Stouffer & Bierregaard 1995, Şekercioğlu et al 2002, Moloney 2005, Sekercioglu 2007, Sodhi et al 2011, Visco & Sherry 2015). These impacts include crowding within remaining habitat, as displaced individuals attempt to resettle after deforestation and/or as new recruits that are unable to disperse attempt to enter the breeding population (Bierregaard & Lovejoy 1989, Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). The resulting increase in population density is known to alter intra- and inter-specific interactions and other density-dependent processes that, in turn, negatively impact individual fitness and ultimately long-term population viability (Zanette 2000, Fasce et al 2011, Sodhi et al 2011).

Compared with the literature, no evidence of post-fragmentation crowding was found in the PYR populations studied. Instead, PYRs appear to be indifferent to decreased fragment size, with populations exhibiting remarkably consistent densities, territory characteristics, and behaviour throughout continuous forest and fragments of all sizes. Based on the literature, I predicted there would be an increase in the number of groups and individuals per ha as fragment-size class decreased. Contrary to this, population densities (group and individual) did not change. My data showed there are approximately one group, and two birds,

per two hectares of forest in all fragment-size classes. I also predicted that PYR territory characteristics would change due to increased population density, and expected to find a decrease in territory size, regularity of shape, and inter-territory distances as fragment size decreased. Instead, no evidence to support any of these predictions was found. Across all fragment-size classes PYR territories were consistently around 0.8 hectares in size, and ~1.7 times as long as they were wide (mean: 126 x 78 m). Similarly, the distances between territories did not vary as fragment size decreased. The same clustered arrangement of territories was seen in all fragment-size classes, with greater variation in distances between clusters occurring only in large fragments.

Finally, I predicted that PYR aggressive territory defence behaviour would increase in intensity (shorter response time / more defenders / more vocalisation) as fragment size decreased. Again, I found no evidence to support this. The rate of vocalisation was consistent across all fragment sizes, with defenders vocalising ~40% of the time. Similarly, while the number of territory defenders differed significantly between fragments of different sizes, these differences were not consistent with crowding effects (i.e. increasing number of defenders as fragment size decreases). Generally, territory defence by a single bird, or more than one bird, was just as likely in small, medium and continuous fragment-size classes. In large fragments, investment in territory defence was actually lower, with territory defence usually being undertaken by just a single bird. This result is consistent with large fragments tending to have large inter-territory distances more often than other fragment-size classes. Greater 'enemy-free' space between territories reduces the intensity of conspecific aggression, which would likely have some bearing on why investment in territory defence was lower in large fragments (Brown 1964, Jeffries & Lawton 1984, Eason & Hannon 1994, Yoon et al 2012, Lebeuf & Giroux 2014, Bhardwaj et al 2015, Bregman et al 2015, Davies & Sewall 2016).

These results contradict expectations based on the current literature on the usual nature and extent of post-fragmentation impacts on rainforest understory insectivores. Given these findings, it was concluded that the first hypothesis was problematic, and PYRs were not exhibiting negative effects of post-fragmentation crowding within remaining rainforest remnants (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). Habitat clearing and fragmentation on the Atherton Tablelands region occurred throughout the early 20th century, culminating between 40–60 years ago (Kanowski et al 2003, Evans & Evans 2017). Therefore, while temporary crowding in remaining habitat might have occurred soon after fragmentation, my research indicated that the phenomenon is not in effect now.

This required a change in the direction of my research. First, there was no further need to look for more subtle density-dependent effects, including upregulation in secretion of the ‘stress hormone’ corticosterone (Creel et al 2013, Viblanc et al 2014, Newman et al 2015, Blondel et al 2016), which would only have been useful had evidence of post-fragmentation crowding been found. Second, these findings led me to test the alternative hypothesis involving the possibility that PYRs may be fragmentation ‘winners’ or, at the very least, fragmentation ‘indifferent’, as discussed in Chapter 2.

In conclusion, contrary to the literature, PYR populations on the Atherton Tablelands are not experiencing crowding or the associated density-dependent impacts that other understory insectivores experience after habitat fragmentation. This begs the question, if the literature does not hold true for this species, what does this mean for our broader understanding of the impacts of habitat loss and fragmentation on other rainforest understory insectivores? And how should it inform our approach to managing similar species, populations, and communities? To answer this, the generality of the results obtained for PYRs need to be more

fully tested on other species to identify whether there is a more general resilience to the impacts of habitat fragmentation in other species on the Atherton Tablelands, or even the wider Wet Tropics bioregion than the current literature would suggest (Moloney 2005, Şekercioğlu 2007). These findings also contribute to our knowledge of PYR ecology and demonstrate that the species is a good model for understanding the effects of habitat fragmentation on tropical rainforest understory birds, because they offer an alternative condition rather than further support for the current paradigm.

CHAPTER 2

HABITAT SPECIALISATION AND COOPERATIVE BREEDING FACILITATES THE PERSISTENCE OF AN UNDERSTORY INSECTIVORE IN RAINFOREST FRAGMENTS (*Tregellasia capito*)

ABSTRACT

Understory insectivores are particularly sensitive to the impacts of habitat fragmentation. As a consequence, they are being lost from rainforest communities globally. However, habitat fragmentation is not negative for all species and some adapt well to, or even benefit from, changed conditions. The Pale-yellow Robin (PYR) *Tregellasia capito* is a territorial, understory insectivore known to inhabit continuous forest and small fragments where other species have been lost. A previous study (Chapter 1) on PYR sensitivity to habitat fragmentation found they were indifferent to habitat fragmentation. Therefore, an alternative hypothesis warranted testing. According to the literature, the persistence of PYRs might be explained by traits that confer protective or competitive advantages (i.e. cooperative breeding, habitat specialisation, and competitive exclusion). I hypothesised that PYRs would cooperatively breed to offset a lack of individual breeding opportunities in saturated habitat and maximise non-uniform distribution of resources. Also, that PYR presence would be associated with preferred habitat characteristics. To test this, PYR populations in 16 complex notophyll vine forest sites on the Atherton Tablelands were studied (four fragment-size classes, each with four sites: >501 ha, >51 ha to 500 ha, 26–50 ha). ≥16 territories were surveyed in each class ($n = \geq 64$). To gauge the incidence of cooperative breeding, PYR territories were mapped, and the number of individuals in each was determined. Comparisons were made between fragment-size classes to detect differences in

group size. Spot-sampled habitat surveys ($n = 112$) were conducted, and 15 habitat variables were measured. The relationship between PYR presence / absence and habitat variables was assessed to detect habitat specialisation. It was found that PYRs cooperatively breed throughout fragments of all sizes, with no increase in incidence as fragment size decreased. Density of stems per m^2 and 'wait-a-while' – which are both abundant features of disturbed habitat – were found to be significantly related to PYR presence / absence. As such, it was concluded that PYRs are disturbed habitat specialists able to utilise a cooperative breeding strategy in response to dispersal limitations, and habitat changes associated with habitat fragmentation.

INTRODUCTION

Background

The literature suggests that understory insectivores are especially sensitive to the impacts of habitat fragmentation and, consequently, are being lost disproportionately from rainforest communities globally (Stouffer & Bierregaard 1995, Şekercioğlu et al 2002, Moloney 2005, Şekercioğlu 2007, Sodhi et al 2011, Visco & Sherry 2015). A review of this literature led me to develop two principal hypotheses concerning why Pale-yellow Robins (PYR) *Tregellasia capito* are able to persist in rainforest fragments while other species cannot. In Chapter 1, I tested the first and most likely of these hypotheses based on previously available evidence, i.e. that habitat fragmentation causes crowding and an associated up-scaling of intra-specific aggression in PYRs, a phenomena that may not be immediately detrimental but become increasingly problematic in the longer term (Ewers & Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). However, contrary to the literature, I found no evidence of either crowding or increased intra-specific aggression (Chapter 1). At the very least, the PYR populations I studied appeared indifferent to the effects of habitat fragmentation.

Typically, species that are area-sensitive, interior-dwelling, sedentary, insectivorous, territorial, rare, or have low fecundity or dispersal ability, are consistently more susceptible to negative impacts than others (Warburton 1997, Ford et al 2001, Moloney 2005, Ewers & Didham 2006, Korfanta et al 2012, Newbold et al 2014, Cornils et al 2015, Visco et al 2015). In contrast, habitat disturbance has a negligible or beneficial effect on species that are generalist, highly fecund, abundant, able to use forest edges and the matrix, granivorous and frugivorous, highly mobile, cooperative breeders, and superior competitors (Bender et al 1998, Matter 2000, Fahrig 2003, Maas et al 2009, Boscolo & Metzger 2011). Importantly, PYRs are anomalous in that they do not fit clearly into either of these

two broad life-history types. For example, they are rainforest dependent understory insectivores, but they are not area sensitive and they are not strictly interior-dwelling, as many negatively impacted species are. Also, they are relatively abundant, able to use forest edges and the matrix (pers. obs.) and, known to cooperatively breed (Male 2000, Higgins & Peter).

This points to the need to test the alternative hypothesis. Specifically, that PYRs are able to persist in fragments where other species are lost owing to certain species-specific traits that confer protective or competitive advantages, for example: cooperative breeding (Cooper 2000, Male 2000, Koenig & Dickinson 2004, Stevens et al 2015, Husemann et al 2015, Langmore et al 2016); habitat specialisation (Stouffer & Bierregaard 1995, Ford et al 2001, Ewers & Didham 2006); and, competitive exclusion (Diamond 1973, Ewers & Didham 2006, Stevens et al 2015, Bennett et al 2015, Kutt et al 2016) (Fig 0.1). The scope of this study included cooperative breeding and habitat specialisation. Competitive exclusion was not tested for practical reasons.

Cooperative breeding

Habitat fragmentation causes territories to have a more uniform distribution and creates a shortage of unoccupied breeding habitat – referred to as ‘habitat saturation’. A species that possess adaptive flexibility in its reproductive strategy may be less vulnerable to extinction (Komdeur 1992, Koenig & Dickinson 2004, Husemann et al 2015, Langmore et al 2016). One such strategy is cooperative breeding – the evolution of which is closely linked to sensitivity to habitat quality (Komdeur 1992, Koenig & Dickinson 2004). Cooperative breeding is characterised by natal philopatry, delayed dispersal and reproduction, and offspring of both sexes helping parents raise subsequent broods. Many cooperative breeders share common ecological and life-history characteristics (e.g. extreme philopatry, habitat specialisation, sensitivity to habitat quality, and low mobility) (Komdeur 1992,

Cooper 2000, Koenig & Dickinson 2004, Gusset & Macdonald 2010, Blackmore et al 2011, Husemann et al 2015).

A number of species are known to switch to and use cooperative breeding as a strategy to offset a lack of individual breeding opportunities in saturated habitat or maximise non-uniform resource distributions (e.g. Seychelles warblers *Acrocephalus sechellensis* in Komdeur 1992, Visco et al 2015). For individuals, there is a trade-off between the substantial costs of cooperative breeding (e.g. lack of individual breeding opportunities), and benefits, which may include enhanced survival, indirect fitness gains from helping related individuals, and better opportunities to secure or inherit a high-quality breeding vacancy in the future (Cooper 2000, Gusset & Macdonald 2010, Kingma et al 2014, Keynan & Ridley 2016). For groups, the number of available carers positively influences reproductive success through enhanced food provisioning, parental and/or sentry duties, and predator defence (Cooper 2000, Male 2000, Grabowska-Zhang et al 2012, Stevens et al 2015, Blondel et al 2016, Keynan & Ridley 2016, Langmore et al 2016).

When breeding, PYRs can be found both in pairs, or in groups of one dominant male, with one or two females and one or two subordinate males that may be related to the adults (Male 2000, Higgins & Peter 2002, Birds in Backyards 2016). However, whether this breeding strategy is a direct adaptive response to the dispersal limitations caused by habitat fragmentation is unknown.

Habitat requirements

The ability of habitat to meet a species' specialist needs is a contributor to individual fitness, and so can play a key role in a species' sensitivity to disturbance and vulnerability to extinction (Zanette 2001, Briggs et al 2007, Johnson 2007, Visco et al 2015). If fragments contain appropriate quality habitat in sufficient quantity to maintain viable breeding populations of a particular species, the impacts

of fragmentation will not be immediately apparent on short-term behaviour, or measures of reproductive success (Şekercioğlu et al 2002, Chama et al 2013, Stratford & Stouffer 2013, Correll et al 2016, Terraube et al 2016). Such impacts would instead be due to the lack of dispersal and recruitment opportunities associated with overall loss of habitat, rather than to the influence of fragmentation per se. Habitat specialisation of this type could explain the persistence of PYRs within rainforest fragments without obvious crowding effects being apparent (Ford et al 2001, Moloney 2005, Stratford & Stouffer 2013, dos Anjos et al 2015, Kutt et al 2016).

Overview of chapter

The aim of this study was to determine whether PYRs possess life-history traits that confer a competitive advantage or protect against extinction risk in fragmented landscapes. Specifically, I investigated if they utilise a cooperative breeding strategy in direct response to environmental conditions, and/or if they display a preference for habitat characteristics or resources that are consistently available within rainforest fragments. To this end, I mapped PYR territories, and collected data on the number of individuals in each territory to establish the degree of PYR cooperative breeding across rainforest fragments of different sizes. I also conducted habitat surveys to identify if the presence or absence of PYR territories was related to any specific habitat characteristics or resources.

METHODS

Study sites and sampling design

To determine if PYRs possess traits that may enable them to persist in fragmented habitat, I used the same 16 rainforest study sites grouped into four fragment-size classes as described in Chapter 1 – Methods. At these sites, I quantified the

incidence of PYR cooperative breeding, and whether specific habitat characteristics were associated with PYR presence or absence by determining the number of individuals in at least 16 PYR groups in each fragment-size class (≥ 4 groups in each of the 16 sites, $n = \geq 64$), and by conducting ≥ 12 paired (1 x PYR present, and 1 x PYR absent) habitat surveys in each of the four fragment-size classes ($n = \geq 112$) (Appendix A: *Schedule of study sites*, Appendix B: *Study sites map*). The comparison of paired presence / absence surveys at each site was to account for any potential variation between sites.

Group size

To determine if the PYR cooperative breeding strategy is a direct adaptive response to the dispersal limitations caused by habitat fragmentation, I collected data on the number of birds engaging in territory defence within each territory (as described in Chapter 1 – Methods). ‘Group size’ was determined as the maximum number of adult PYRs observed at any one time within a territory during the territory mapping process.

Habitat surveys

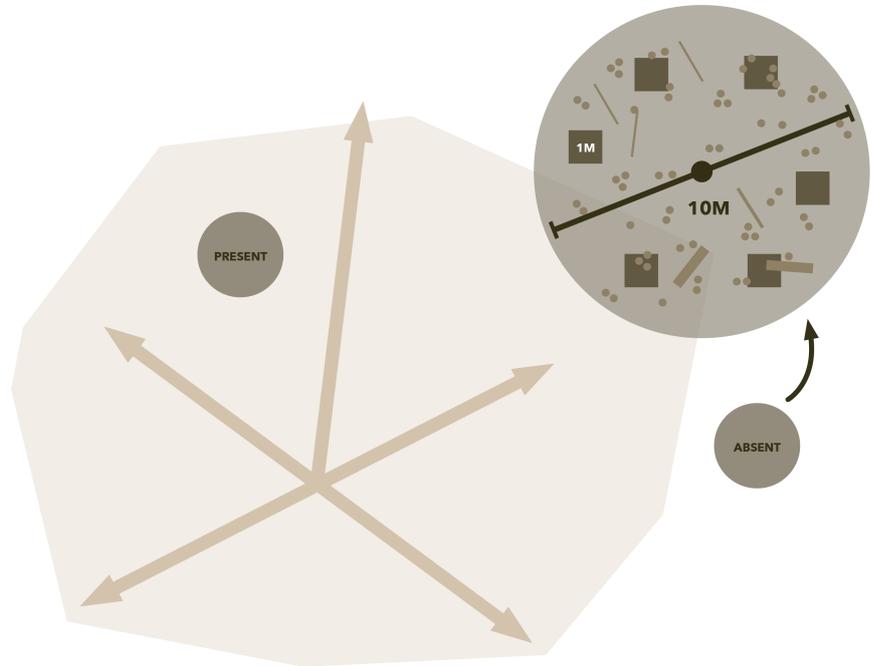
Usually, a comprehensive transect-based survey methodology would be employed to fully describe vegetation characteristics (Bibby et al 1988, Kanowski et al 2003, Gillison 2006, Catterall et al 2008, Kanowski et al 2010, Cornils et al 2015, Stevens et al 2015). With time and resources a key consideration, I developed a spot-sampling habitat survey methodology based on many of the variables measured in transect-based methodologies, that could be conducted quickly and consistently whilst simultaneously mapping PYR territories (as described in Chapter 1 – Methods). Habitat survey locations were selected at random within and outside known PYR territories. To commence a survey, a circular survey site of ~ 5 m radius was established (~ 78.5 m²). For each survey, 15 variables were measured: PYR presence / absence, canopy cover, understory (<2 m) density, stems per m²,

'wait-a-while' (*Calamus* sp.). presence / absence, tree-falls, edge, gully, slope, coarse woody debris in three size categories, buttress roots, and leaf litter cover and depth (Fig. 2.1).

First, PYR presence or absence was confirmed using playback (as described in Chapter 1 – Methods). Absence was verified when no bird was detected after two consecutive five-minute calling periods. Next, overhead canopy cover was determined based on a visual estimation of 'percent cover' via a quick reference sheet ($\pm 10\%$) (Swiecki & Bernhardt 2001). Understory (<2 m) density was visually assessed and described as either 'open', 'medium', or 'dense' using three reference site photographs (Cornils et al 2015) (Appendix E: *Understory <2 m density*). Stems per m^2 was determined by counting the total number of woody stems in six $1\ m^2$ quadrats placed in randomly selected locations in the survey area. The mean number of stems per m^2 was then calculated for each survey site. Presence or absence of 'wait-a-while', and any recent tree-falls were recorded as 'yes' or 'no'. Whether the forest edge was within the survey area was recorded as 'yes' or 'no'. Similarly, whether the survey site was in a gully was recorded as 'yes' or 'no'. To determine slope of the ground I used a 5 m piece of string and pocket spirit level to measure a run between the centre and edge of the survey area in a level line above to the ground, and measured any resulting rise with a tape measure ($\pm 1\ cm$). The direction perceived to have the greatest slope was chosen to make the measurement. Slope was calculated as $\text{rise} / \text{run} * 100$. A count of coarse woody debris in three fragment-size categories ('<30 cm', '30–60 cm', '>60 cm') was also made for the entire survey site. Next, the presence or absence of buttress roots was recorded as 'yes' or 'no'. Finally, measurements of leaf litter % cover and depth were taken within a $30\ cm^2$ quadrat placed in six randomly selected locations in the survey site. The percentage of leaf litter cover was estimated ($\pm 10\%$) by comparing the amount of bare ground visible to leaf litter, and

a ruler was used to measure litter depth (± 1 cm) in the centre of the quadrat. The mean value for both variables was then calculated for each survey site.

Figure 2.1: Habitat specialisation was tested by conducting paired (PYR present / PYR absent) spot-sampled habitat surveys to detect the species' preference for any one or more of 14 habitat variables: Canopy cover, understory (<2 m) density, stems per m^2 , 'wait-a-while' (*Calamus* sp.) presence / absence, tree-falls, edge, gully, slope, coarse woody debris in three size categories, buttress roots, and leaf litter cover and depth.



Data analyses

Group size

I analysed PYR group size to understand if breeding strategy differed between fragments of different sizes. I grouped the number of adult birds in each territory into ≤ 2 and > 2 , where more than two adult birds per group indicated cooperative breeding. The data were analysed using a chi-squared test implemented in S-Plus (TIBCO Software Inc. 2017), to determine if the frequency of groups with >2 adult birds was higher than expected in any fragment-size class.

Habitat surveys

I analysed the habitat survey data to determine if certain habitat features or characteristics were related to the presence or absence of PYRs. First, I standardised numerical data $((x - \text{mean}(x)) / \text{SD}(x))$ to prevent undue influence of

any explanatory variable due to the large range of values and units in the data (Campbell 2016). Prior to generating each statistical model, I checked for correlated predictor variables (Zuur et al 2010). Consequently, understory (<2 m) density was excluded from analysis due to its high correlation with stems per m². I then ran a Generalised Linear Mixed-effects Model (GLMER) in RStudio (R Core Team 2017, RStudio 2017) using the 'glmer' function in the 'lme4' package (Bolker 2017). Each model fitted PYR presence / absence as a function of canopy cover, stems per m², wait-a-while, tree-fall, edge, gully, slope, coarse woody debris <30 cm, coarse woody debris 30–60 cm, coarse woody debris >60 cm, buttress roots, leaf litter cover, and leaf litter depth. 'Site' was specified as a random-effect grouping variable, and the link function as 'binomial', as is appropriate for the presence / absence response variable. Model selection was performed using backwards, stepwise regression (Campbell 2016), with selection based on the lowest AIC model values using the 'drop 1' function. The most parsimonious model was defined as that which included the minimum number of terms to produce the best possible explanation of the response variable (lowest AIC value), and may or may not have contained traditionally significant (P <0.05) variables (Campbell 2016).

After considering the habitat survey analysis results (presented below), I hypothesised that the density of stems might provide an explanation for why large fragments appeared anomalous in several results presented in Chapter 1. In order to test this, I used a Linear Mixed-effects Model (LMM) to test for differences in stem densities between fragment-size classes in RStudio (R Core Team 2017, RStudio 2017). Heterogeneity of variance in the residuals from each fragment-size class was accounted for specifying the 'varIdent' function from the 'nlme' package (R-core R-core@R-project.org 2009), which allows data in each fragment-size class to have its own unique variance structure. 'Site' was specified as a random-effect grouping variable.

As a consequence of the habitat survey analysis results (presented below), I wanted to test if the presence of 'wait-a-while' varied across fragments of different size, as this may also help to explain previous results (Chapter 1). To test if 'wait-a-while' presence / absence differed more than would be expected in any fragment-size class I analysed the presence / absence frequency counts across each fragment-size class using a chi-squared test in S-Plus (TIBCO Software Inc. 2017).

RESULTS

Group size

PYR group size did not vary between fragments of different sizes ($\chi^2 = 7.44$, $df = 3$, $P = 0.059$). PYRs used both a single-pair and cooperative breeding strategy in all fragment-size classes with the incidence of cooperative breeding being independent of fragment size. In general, there were two or three birds per territory. Group sizes of up to five individuals were recorded. The mean number of individuals per group was 3.06 (SD \pm 0.97) in small fragments, 2.19 (SD \pm 0.66) in medium, 2.29 (SD \pm 0.59) in large, and 2.88 (SD \pm 1.09) in continuous forest (Fig. 2.2).

Habitat surveys

PYR presence was significantly and positively related to the number of stems per m^2 and the presence of 'wait-a-while'. Of these two variables, stems per m^2 had the strongest influence on PYR presence (Table 2.1). No other factors were found to be significant.

Table 2.1. The most parsimonious Generalised Linear Mixed Model (GLMM) (binomial) by maximum likelihood (Laplace Approximation) for the influence of habitat characteristics on PYR presence / absence. All explanatory variables were standardised prior to the analysis $((x - \text{mean}(x)) / \text{SD}(x))$.

	Estimate	SE	Z value	P
Intercept	-1.67	0.6	-2.8	0.0052
Stems per m ²	0.36	0.11	3.15	0.0017
Wait-a-while	1.49	0.55	2.7	0.0069

The density of stems per m² differed significantly between fragment-size classes (LMM: $F_{(3,9)} = 4.076$, $P = 0.044$). There was a tendency for there to be more areas of low stem density in small and large fragments, with the lowest stem densities found in large fragments. Mean number of stems per m² was 3.0 (SD \pm 1.44) in small fragments, 4.25 (SD \pm 2.47) in medium, 2.72 (SD \pm 1.40) in large, and 5.27 (SD \pm 1.88) in continuous forest (Fig. 2.3).

Presence of 'wait-a-while' in the habitat survey plots differed significantly between fragments of different sizes ($\chi^2 = 22.44$, $df = 3$, $P = <0.0001$). The frequency of encountering 'wait-a-while' decreased as fragment size increased. 'Wait-a-while' was present in 100% of small fragment habitat surveys ($n = 26$), 93% of medium fragment habitat surveys ($n = 28$), 72% of large fragment habitat surveys ($n = 25$), and 55% of continuous forest habitat surveys ($n = 33$) (Fig. 2.4).

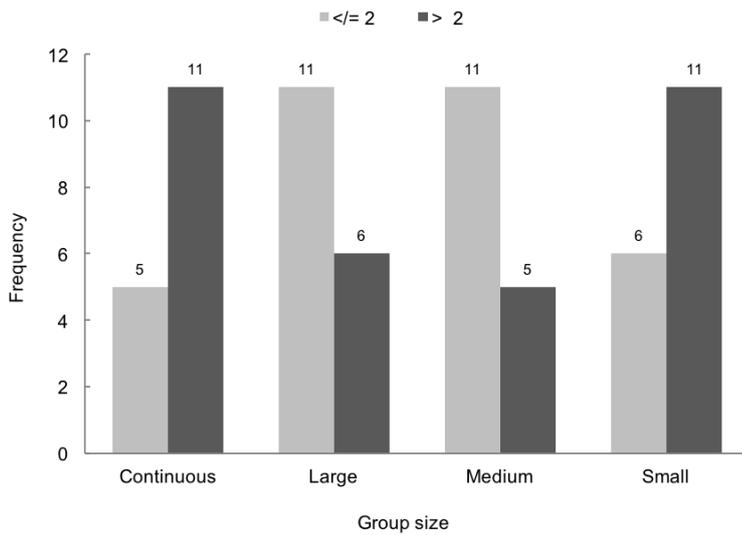


Figure 2.2: Frequency of group sizes ≤ 2 and > 2 birds per group. Group size recorded as the maximum number of birds seen at any one time in the territory ($n = 66$). The frequency of groups over 2 birds was not greater than would be expected in any fragment-size class ($\chi^2 = 7.44$, $df = 3$, $P = 0.059$). PYRs used both a single-pair and cooperative breeding strategy in all fragment-size classes.

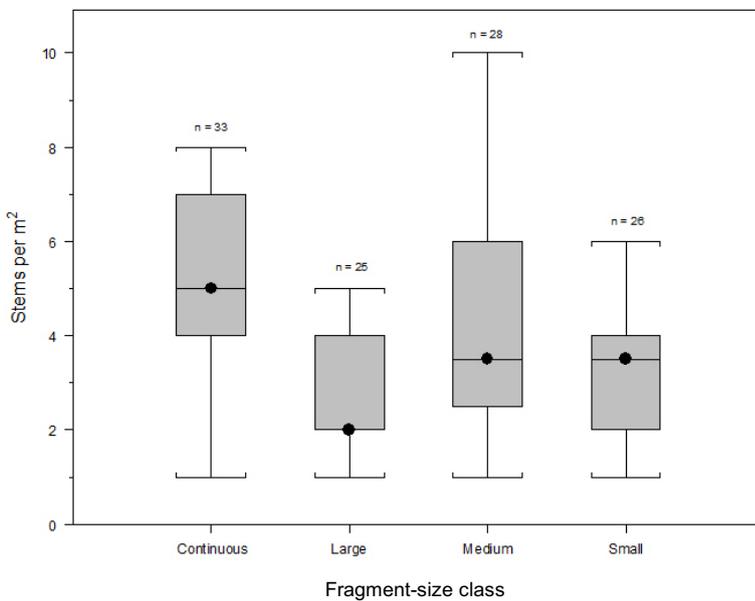


Figure 2.3: The density of stems per m^2 differed significantly between fragment-size classes (LMM: $P = 0.044$) ($n = 112$). There was a tendency for there to be more areas of low stem density in small and large fragments, with the lowest stem densities found in large fragments. Mean: small 3.0 (SD ± 1.44) ($n = 26$), medium 4.25 (SD ± 2.47) ($n = 28$), large 2.72 (SD ± 1.40) ($n = 25$), continuous 5.27 (SD ± 1.88) ($n = 33$).

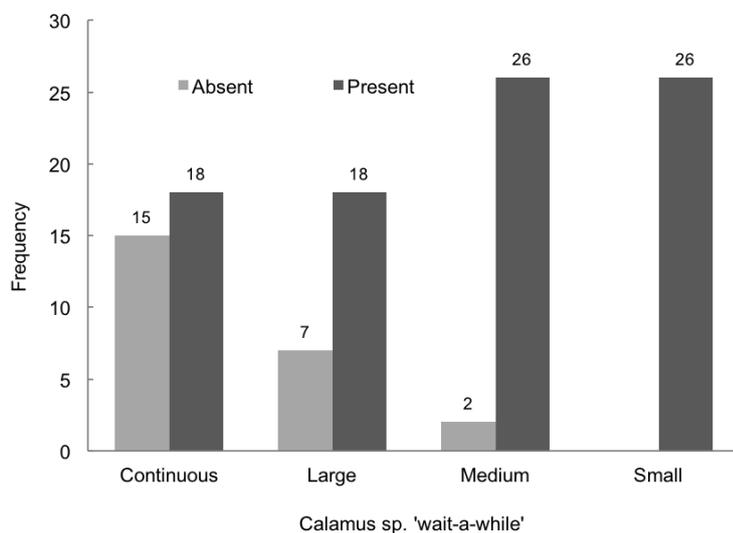


Figure 2.4: Frequency of *Calamus* sp. 'wait-a-while' presence / absence ($n = 112$). Presence of 'wait-a-while' differed significantly between different fragment-size classes ($\chi^2 = 22.44$, $df = 3$, $P = < 0.0001$), and the chance of encountering 'wait-a-while' decreased as fragment size increased. Presence: Small 100% ($n = 26$), medium 93% ($n = 28$), large 72% ($n = 25$), continuous 55% ($n = 33$).

DISCUSSION

Results from studies detailed in Chapter 1 demonstrated that PYRs were not experiencing crowding or the associated density-dependent impacts that negatively affect other understory insectivores after habitat fragmentation. Therefore, I tested the alternative possibility that PYRs possess certain traits known to promote persistence in rainforest fragments, such as a cooperative breeding strategy (Komdeur 1992, Koenig & Dickinson 2004, Husemann et al 2015, Langmore et al 2016), or a preference for conditions that are inherently abundant in fragmented habitats (Ford et al 2001, Zarette 2001, Moloney 2005, Briggs et al 2007, Johnson 2007, Kutt et al 2016).

While the species' ability to cooperatively breed is documented in the literature, it was not known if the frequency of this behaviour increased in direct response to the process of fragmentation. Similarly, the species' use of both forest edge and interior habitats is also well documented, but whether this pattern of habitat use was preferential, or simply a consequence of limited alternative opportunities was unknown. Therefore, the primary aim of this chapter was twofold. First, to determine if PYR populations on the Atherton Tablelands were adjusting their breeding strategy in response to decreasing fragment size and, second, to identify if any habitat variables were positively related to the presence or absence of PYR breeding territories.

PYRs were found to be breeding both as individual pairs and as cooperative groups in equivalent ratios throughout all fragment sizes. Thus, it is unlikely that PYRs adopt a cooperative breeding strategy as a direct adaptive response to the dispersal limitations caused by habitat fragmentation (as per Komdeur 1992). In general, there were two or three birds per territory, but group sizes of up to five individuals were recorded. These findings are consistent with other published

studies on patterns of cooperative breeding in the species (Male 2000, Higgins & Peter 2002).

The presence / absence of PYRs was significantly and positively related to both stem density and the presence of 'wait-a-while'. Of these, stem density had the strongest influence. Stem density also differed significantly between fragment-size classes, with large fragments having the lowest stem densities. The presence of 'wait-a-while' also differed significantly between fragment-size classes, with it becoming more abundant as fragment size decreased. As in Chapter 1, large fragments were again anomalous. The reason for lower stem density and less 'wait-a-while' presence in large fragments is likely associated with the management history of these fragments, whereby intensive management impedes the development of an understory (Bibby et al 1988, Kanowski et al 2003). Importantly, the lower abundance of preferred resources (i.e. 'wait-a-while') and conditions (i.e. dense vegetation) in large fragments provides a likely explanation for the tendency towards lower PYR population densities, more variable inter-territory distances, and lower territory defence investment in large fragments, as previously identified in Chapter 1.

My results suggest that PYRs possess two traits known to facilitate persistence in fragmented and degraded forest habitats. First, they can utilise a cooperative breeding strategy that may buffer them against dispersal limitation, by allowing them to better exploit areas of quality-habitat, rear more broods, better defend territories, and reduce the risk of predation – all factors which ultimately make them less vulnerable to extinction (Komdeur 1992, Koenig & Dickinson 2004, Husemann et al 2015, Visco et al 2015). Second, they preferentially establish breeding territories in dense and complex vegetation where post-disturbance colonising plant species such as 'wait-a-while' are in abundance (Tracey & CSIRO 1982, Moloney 2005, Stratford & Stouffer 2013, Campbell 2016). The Wet Tropics region has had

a highly dynamic past e.g. Pleistocene contraction and expansion of rainforest and regular highly disturbing cyclonic events (Moloney 2005, Catterall et al 2008, Freeman et al 2008). Consequently, it has been hypothesised that some of its inhabitants may have evolved lowered sensitivity to, and even an ability to exploit, disturbed habitats (Moloney 2005, Şekercioğlu 2007, Pavlacky et al 2015, Powell et al 2015). If this is the case for the PYR, anthropogenic rainforest fragmentation may represent the upscaling of natural disturbance processes that create and maintain preferred PYR habitat (Moloney 2005, Catterall et al 2008, Cornils et al 2015).

Contrary to the literature, this means PYRs are an understory insectivore that may actually benefit from these usually detrimental processes (Cornils et al 2015, Powell et al 2015). This raises the question of whether PYRs are an anomalous case, or whether other species that exist in rainforest fragments with them are also pre-adapted to disturbed habitat. To answer this, further studies on the prevalence of similar habitat specialisation and cooperative breeding behavior amongst other species in rainforest fragments across the Atherton Tablelands, and the wider Wet Tropics bioregion are warranted.

In conclusion, the results of the current study suggest that PYRs preferentially breed in habitat that is consistently available in rainforest fragments, and that the species may even be a 'disturbed habitat' specialist (Cornils et al 2015). Thus, the processes of degradation associated with habitat fragmentation, which are usually detrimental to other bird species, may favour PYRs. And where these conditions are present, PYRs can also utilise a cooperative breeding strategy to offset, to some degree, problems of dispersal limitation (Komdeur 1992). To the best of my knowledge, documented examples of habitat specialisation facilitating persistence of understory insectivores in fragments are extremely rare – particularly if persistence is several decades post-fragmentation (e.g. Thrush-like antpittas

Myrmothera campanisona in Stratford & Stouffer 2013, Chestnut-backed antbird *Myrmeciza exsul* in Visco & Sherry 2015, Powell et al 2015). Thus, the PYR presents a unique opportunity to better understand the impacts of habitat fragmentation on understory insectivores, and the synergies between cooperative breeding, habitat quality, and habitat specialisation. Finally, these findings suggest that a less intensive management strategy may be required for this species than would be suggested by the literature.

GENERAL DISCUSSION

PYRs persist in small rainforest fragments

The aim of this study was to contribute to our knowledge of species-level responses to habitat fragmentation, with a focus on understory insectivores – a group of birds that, by all accounts, are disproportionately impacted by habitat loss and degradation around the world (Stouffer & Bierregaard 1995, Warburton 1997, Şekercioglu et al 2002, Moloney 2005, Sekercioglu 2007, Sodhi et al 2011, dos Anjos et al 2015, Visco & Sherry 2015). More specifically, my aim was to examine the persistence of PYRs in rainforest fragments on the Atherton Tablelands to better understand their long-term population viability.

Based on a review of the literature, I formulated two principal hypotheses to explain what might be occurring within PYR populations on the Atherton Tablelands. The first hypothesis was that they persist in increasingly crowded conditions as patch size reduces, with negative impacts on their long-term existence. The second was that their persistence in fragments could be long-term, facilitated by traits that allowed them to mitigate or exploit post-fragmentation conditions and processes that are normally detrimental to other species. Based on an overwhelming body of evidence demonstrating that rainforest understory insectivores are extremely sensitive to the impacts of habitat fragmentation, I predicted that the first hypothesis would be the most likely in the case of PYRs.

PYRs are indifferent to habitat fragmentation

As detailed in Chapter 1, I found that PYRs were not experiencing post-fragmentation crowding characterised by an increase in population density and changes to density-dependent processes. Based on the literature, I predicted I would detect changes to PYR population densities, territories (size, shape and spatial arrangement), and behaviour (Bierregaard & Lovejoy 1989, Ewers &

Didham 2006, González-Varo et al 2008, Sodhi et al 2011, Pavlacky et al 2015). Instead, I found these characteristics were remarkably consistent across all fragment-size classes.

My analysis showed that, on average, there was one group and two PYRs, per two hectares of forest, across all fragment-size classes. Also, that PYR territories were consistently around 0.8 hectare in size, ~1.7 times as long as they were wide, and in a clustered arrangement. PYR behaviour was similarly consistent across all study sites, with no differences in their response time to playback nor evidence of rate of vocalisation during defence. The only significant difference was in the number of territory defenders, which was found to be lower in large fragments.

These findings demonstrate that, contrary to expectation, PYR populations were not experiencing post-fragmentation crowding. Instead, they appeared to be indifferent to the effects of fragment size due to them operating on a spatial scale smaller than the overall size of most fragments. As such, the loss of total habitat area is more detrimental to PYR populations than the conditions resulting from fragmentation. From these results, I concluded that the second hypothesis warranted further investigation. Unexpectedly, I found that PYRs possess traits that might enable them to persist in small fragments and, to some extent, exploit the conditions inherent to fragmentation that are usually detrimental to other species (Chapter 2). Namely the ability to cooperatively breed, in conjunction with a preference for disturbed habitat that is characterised by an increased density of stems, and the presence of 'wait-a-while' – a highly successful coloniser of disturbed areas (Hausmann 2004, Moloney 2005, Catterall et al 2008).

Furthermore, my analysis found large fragments to be anomalous to varying degrees in several instances (i.e. a tendency to have lower territory densities, greater variation in inter-territory distances, lower investment in territory defence,

and more vocalisation when defending territories). Large fragments also had the lowest stem densities, and less 'wait-a-while' than smaller fragments. A difference between the large fragments and other sites was anecdotally noted during field work. The sites were much easier to move through, with a more sparse understory, significantly less 'wait-a-while' and dense thickets of other vegetation. It was often much harder to detect potential territories to map, and a significant amount of time was spent walking and playing back calls with no response.

The relationship between habitat availability and PYR population characteristics was more evident in large fragments. A lack of preferred habitat results in fewer territories in a more heterogeneous spatial arrangement. This results in fewer neighbours and less frequent intrusions, requiring less investment in territory defence. As a result, PYRs become more aggressive towards the rare intruder (Brown 1964, Eason & Hannon 1994, Fasce et al 2011, Yoon et al 2012, Lebeuf & Giroux 2014, Bhardwaj et al 2015, Bregman et al 2015, Davies & Sewall 2016). It is difficult, however, to make inferences about whether these particular sites were unusual, or if larger fragments generally offer less preferred habitat. For this, a detailed analysis is required of site context and condition and/or disturbance and management history (Bibby et al 1988, Cornils et al 2015, Freeman et al 2015).

A disturbed habitat specialist

The literature consistently states that understory insectivores are at the highest risk from the negative effects of habitat fragmentation, and suffer the highest rates of extinction of all rainforest birds. While this is true for most species, there are exceptions (Stratford & Stouffer 2013, Visco & Sherry 2015). Unlike most other understory insectivores – which are area-sensitive, highly specialised, strictly interior-dwelling, sedentary, and have low dispersal ability (Warburton 1997, Ford et al 2001, Moloney 2005, Ewers & Didham 2006, Korfanta et al 2012, Newbold et al 2014, Cornils et al 2015, Visco et al 2015) – PYRs are relatively abundant,

cooperatively breed, and are able to use forest edges and the matrix (Bender et al 1998, Matter 2000, Fahrig 2003, Ewers & Didham 2006, Maas et al 2009, Boscolo & Metzger 2011). In addition to this, my research shows they specialise on habitat characteristics actually made more abundant by habitat fragmentation and the subsequent process of degradation (Laurance et al 2002, Hausmann 2004, Moloney 2005, Catterall et al 2008, Visco et al 2015, Campbell 2016). It is this atypical combination of traits that likely provides the basis for PYR persistence in rainforest fragments where other species are lost. Thus, PYRs are unlikely to be as at risk of the negative effects of habitat fragmentation and ultimate extinction as the literature would suggest. Instead, deforestation is the greater risk to this species' long-term survival.

Population insights

The PYR is currently listed as Least Concern by the IUCN Red List, but the population has been assessed as likely to be in decline due to the negative effects of habitat loss and fragmentation (BirdLife International 2016). My findings challenge this assessment. Although initial loss of total habitat area is a direct threat to PYR populations (Pavlacky et al 2015), subsequent impacts which typically underpin the eventual extinctions of other species are not a factor likely to impact long-term PYR population viability. In addition, PYR population size has not been quantified (BirdLife International 2016). My results show that PYR population densities and territory characteristics are remarkably consistent throughout continuous forest and fragments, and that their presence / absence is related to specific habitat characteristics. Together, this information could be used as a solid basis for estimating total population and distribution of the species, as well as assessing their long-term survival with a reasonable level of confidence (Bibby et al 1988, dos Anjos et al 2015). By extension, the implications of this for other Australasian robins (family Petroicidae) should be considered, as many are listed by the IUCN as having a decreasing population trend or being threatened with

extinction (BirdLife International 2016). However, many of them share similar traits with the PYR including the ability to cooperatively breed, an ability to utilise forest edges and open areas, and a preference for dense vegetation (Boles 1988, Higgins & Peter 2002, Cousin & Phillips 2008). As such, we may find that other species are similarly less sensitive to habitat fragmentation than the literature suggests.

Management implications

The implications of these findings are potentially applicable to broader landscape management practices. Generally, out of a necessity for efficiency and economy, management of fragmented landscapes makes the base assumption that fragment size is small in relation to a species' actual habitat requirements (Bayard & Elphick 2010). For similar reasons – with the exception of keystone or endangered species – management of specific species in these landscapes is usually underpinned by a focus on life-history traits, with ecological traits a secondary concern (Akçakaya et al 2004, Pukazhenthii et al 2005, Newbold et al 2012). However, my findings would suggest this isn't the ideal strategy for PYRs. In their case, the amount of habitat available is generally going to be greater than what is required to meet their specialised needs (even in small fragments). Also, they do not possess the ecological and life-history traits which typically make understory insectivores sensitive to habitat fragmentation.

These results support the case that an understanding of the spatial scale of species' specialisations, relative to the amount of habitat available, would be beneficial to effectively manage avian communities within fragmented landscapes. To facilitate this, a triage-style risk assessment heat map (Fig. 3.1) could provide a rapid way to assess sensitivity to fragmentation, and prioritise strategic management actions. Ascertaining whether this, or similar assessment and management tools are currently used by land managers, is beyond the scope of this study. However, my results suggest such a tool could be useful.

Limitations

All studies have some limitations, whether that be in the design, data, statistical analysis, or potential impacts. Having carefully considered this, there are a few opportunities to improve future work on the subject. *Territory mapping* – This was labour intensive, so testing to determine the minimum resolution required to get an equivalent level of insight, would make the data collection process much less costly in both time and resources. *Playback* – According to the ‘dear enemy’ hypothesis, the level of familiarity with an intruder may affect intensity of aggressive response (Eason & Hannon 1994, Grabowska-Zhang et al 2012, Yoon et al 2012). In this study, PYR behaviour was assessed using recordings of an unfamiliar intruder. It is difficult to determine if, or how, this might have affected my results without more fully testing the hypothesis as it pertains to PYRs. *Isolation* – A key factor in the impacts of habitat fragmentation on species (Diamond 1973, Bierregaard et al 1992, Stouffer & Bierregaard 1995, Fahrig 2003, Şekercioğlu 2007, Korfanta et al 2012, Stevens et al 2015, Visco et al 2015). This study did not take into account the relative isolation of study sites. Future studies could factor isolation into the design or analysis. *Sampling bias* – An increase in heterogeneity of vegetation structure may have been picked up in large fragments. However, it is difficult to know if this heterogeneity continues with an increase of overall habitat size, because it was difficult to access central areas of the continuous forest sites. While every effort was made to survey at least 250 m away from the forest edge, some edge effects might be present in the continuous fragment-size class data. To test for this, standardised line-transect surveys could be used to measure the heterogeneity of vegetation structure in each of the fragment-size classes. A secondary benefit of this work would be higher resolution data on the abundance of preferred PYR habitat in this vegetation type (Boles 1988). *Temporal context* – My study provides a snapshot of just a single breeding season. It would be beneficial to replicate the study over multiple breeding seasons to establish if this picture of PYR populations is consistent over the long-term.

Further research

There are a few opportunities for further research to validate or expand on the findings this study. They include: *Fine scale impacts* – This study focussed on the indicators that were most likely to exhibit post-fragmentation crowding effects. However, as with many ecological issues, impacts may be much subtler in effect and require detailed studies to detect them. For example, changes in intra- and inter-specific interactions, population demography, stress and body condition, reproductive success, and dispersal. *Competitive exclusion* – In theory, the indifference of PYRs to fragmentation might give them a competitive advantage over other more negatively impacted species. Detailed studies on community composition and inter-species interactions would be required to understand if PYRs are superior competitors within the rainforest community. *New methodologies* – The survey methodologies developed for this study should be assessed against current spot-sampling and transect-based methods to determine if they garner equivalent insights. Improvements to either methodology could be made based on the findings. *Study area* – The scope of this study was limited to just one regional ecosystem type (RE 7.8.4a) to avoid differences in vegetation structure confounding the data (Bibby et al 1988). It would likely be beneficial to test the generality of these findings more widely throughout the species' range to determine if/how their specialist needs are met by other vegetation types, and if any one type better meets their needs. *Generality of the model* – The practical implications of my results are mostly relevant to the PYR. However, if the literature does not ring true for one species, it is conceivable that others are persisting in fragments because they too possess traits that facilitate resilience. Thus, the generality of the model should be tested.

SPECIES RISK ASSESSMENT HEAT MAP

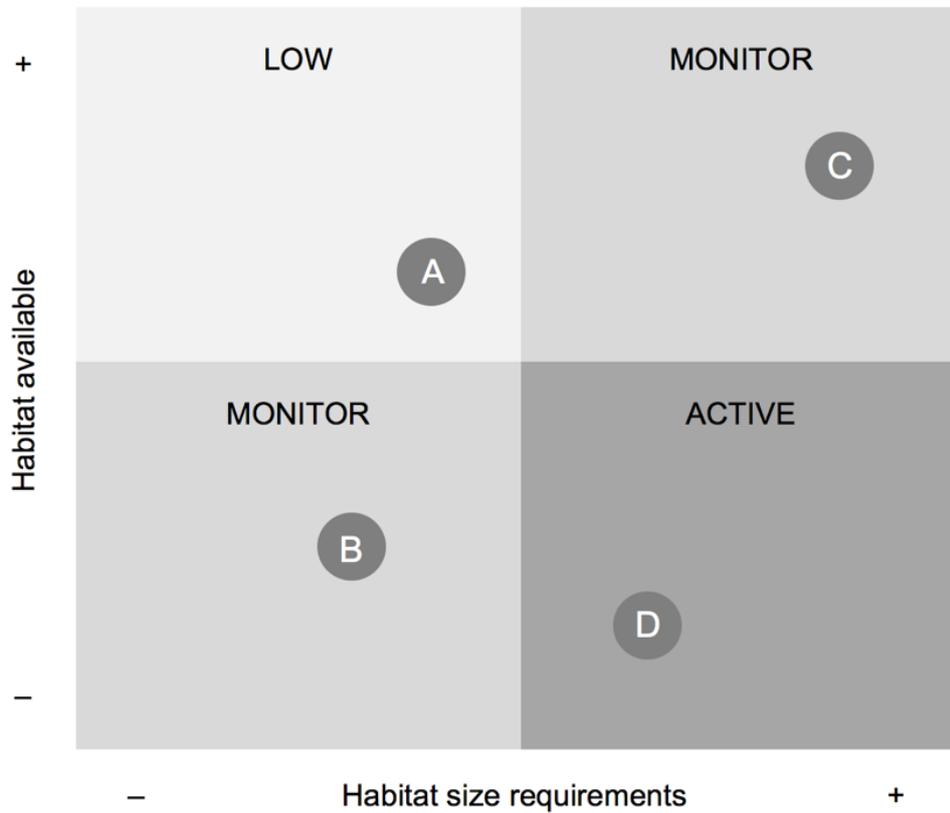


Figure 3.1: Sample species risk assessment heat map. A tool for rapid assessment of species' susceptibility to habitat fragmentation based on spatial scale of species' specialisations, relative to the amount of habitat available, and prioritising strategic management actions e.g. species D has high habitat size requirements, and the amount of habitat available is low. This species is at risk and requires active management. Species A has moderately low habitat size requirements, and availability of habitat is moderate to high. This species requires low management.

CONCLUSION

It is increasingly argued that detailed analyses of species-specific responses to habitat loss and fragmentation will be key to managing and conserving impacted populations and communities (Hammond et al 2015, dos Anjos et al 2015, Hau & Goymann 2015). The key findings reported in this thesis contribute to our understanding of the impacts of habitat fragmentation on understory insectivores and, in particular, the Pale-yellow Robin (PYR) *Tregellasia capito* in two meaningful ways.

First, I found PYR populations on the Atherton Tablelands to be indifferent to habitat fragmentation, and able to persist in fragments with no significant changes to their population densities, territory characteristics, or defence behavior. This finding was contrary to my initial hypothesis. It was also in direct contrast to the literature, which overwhelmingly states that understory insectivores like the PYR should experience a range of negative density-dependent impacts associated with post-fragmentation crowding and isolation.

Second, my studies revealed the PYR to be a disturbed habitat specialist, with the ability to utilise a cooperative breeding strategy to maximise use of preferred habitat. Based on this, it can be concluded that habitat fragmentation is not an existential threat to PYR populations in the Wet Tropics. This finding supported my second hypothesis. As such, this presents a new and rare case of habitat specialisation facilitating post-fragmentation persistence of a rainforest understory insectivore. Further studies are now needed to test the generality of this model.

In addition to this, I have identified two potential practical applications of my findings. First, the results relating to PYR territory densities, characteristics, and habitat preferences, could provide the basis for generating a reasonably accurate estimate of total PYR population size, which is currently unknown (BirdLife International 2016). Second, I have developed a management tool to identify species at risk from the impacts of habitat fragmentation, and assist in the prioritisation of management actions.

In summary, this conceptualisation of the PYR is in line with a relatively recent shift in our perception of rainforests being largely stable environments, towards a greater understanding of their highly dynamic nature. This work further feeds in to the broader discussion around conserving and managing rainforest ecosystems and their inhabitants in more responsive and strategic ways.

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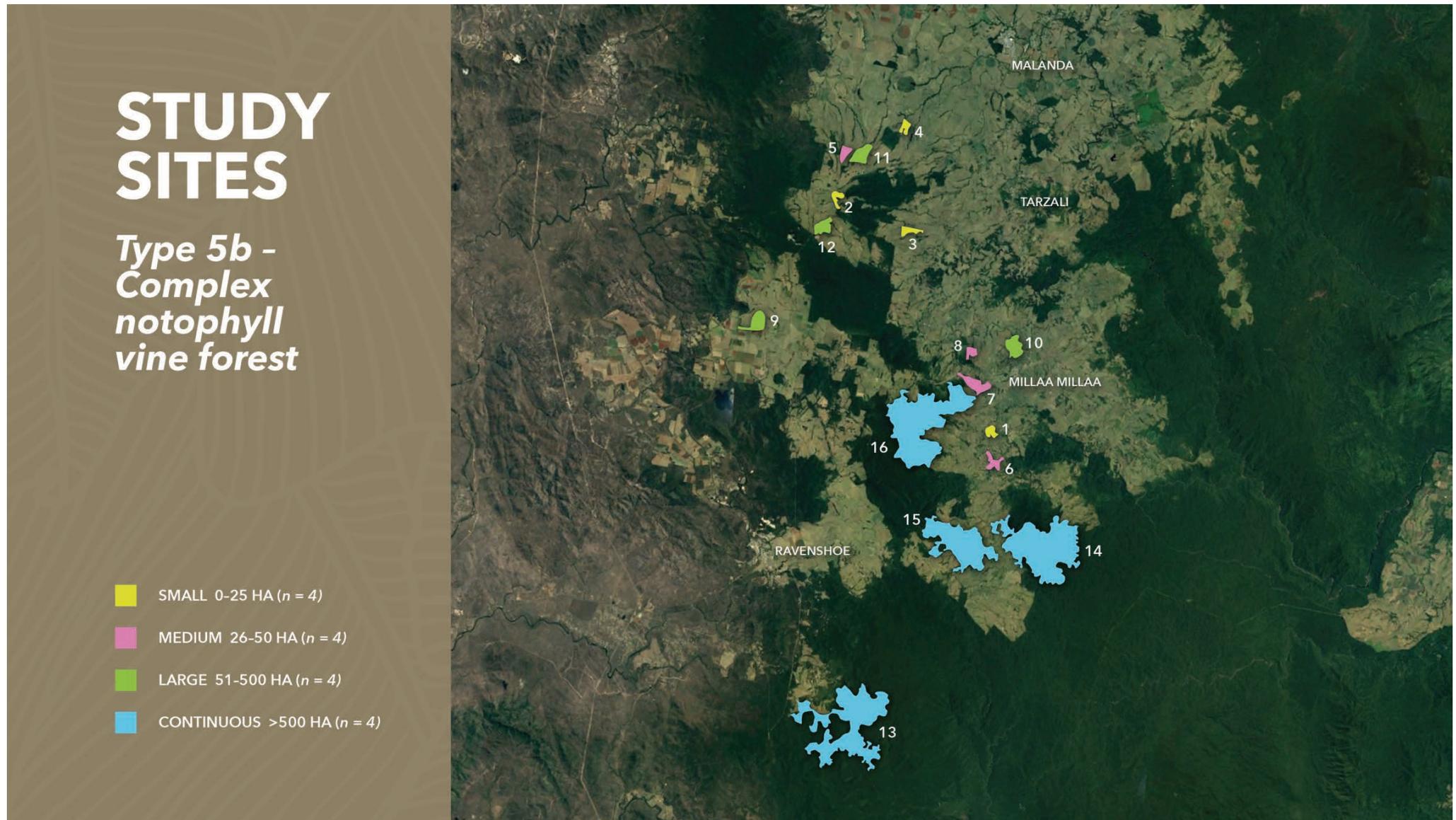
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APPENDIX A: Schedule of sites

ID	LOCODE	CODE NAME	NAME	SIZE (ha)	CATEGORY	LOCALITY	TENURE	NAME	GPS S	GPS E	Elev (m)	RE	TERRITORIES
1	1386S1	PHEASANTRD	Pheasant Road	23	Small	Millaa Millaa / Maalan	Freehold		17°33'07.78"	145°37'13.56"	744	7.8.4a	4
2	1386S2	MCKELLRD	McKell Road	24	Small	Wondecla / Minbun	Freehold		17°26'5.01"S	145°30'33.10"E	1000	7.8.4a	3
3	1386S3	TURNERRD	Turner Road	25	Small	Wondecla / Tarzali	Freehold		17°26'42.48"	145°33'37.80"	784	7.8.4a	5
4	1386S4	NEWLANDSCR	Newland Scrub	24	Small	Wondecla / Malanda	Freehold		17°23'53.43"	145°32'36.66"	820	7.8.4a	4
5	1386M1	BINNIE	Binnie	26	Medium	Wondecla / Malanda	Freehold		17°24'48.44"	145°32'26.40"	813	7.8.4a	5
6	1386M2	WHITEINGRD	Whiteing Road	41	Medium	Millaa Millaa / Maalan	Reserve	Scenic Reserve	17°33'26.72"	145°36'24.36"	785	7.8.4a	5
7	1386M3	EASTEVELYN	East Evelyn Road	46	Medium	Millaa Millaa	Freehold		17°31'13.23"	145°35'33.63"	850	7.8.4a	3
8	1386M4	NEWELLSRD	Newells Road	26	Medium	Millaa Millaa / Moregatta	Freehold		17°30'14.23"	145°35'17.41"	870	7.8.4a	3
9	1386L1	TUMOULINRD	Tumoulin Road	58	Large	Evelyn	Freehold		17°30'02.10"	145°28'27.20"	1105	7.8.4a	1
10	1386L2	MMFALLSSR	Millaa Millaa Falls Scenic Reserve	66	Large	Millaa Millaa	Reserve	Millaa Millaa Falls Park	17°29'59.11"	145°36'46.14"	831	7.8.4a	4
11	1386L3	LUMHOLTZ	Lumholtz's Lodge	61	Large	Wondecla / Malanda	Freehold		17°24'54.90"	145°31'13.26"	880	7.8.4a	7
12	1386L4	ROCKRD	Rock Road	75	Large	Wondecla / Minbun	Freehold		17°27'3.33"	145°30'12.75"	1030	7.8.4a	4
13	1386C1	TULLYFRD	Tully Falls Road	910	Continuous	Ravenshoe	National Park	Tully Falls National Park	17°40'59.64"	145°32'16.79"	1078	7.8.4a	6
14	1386C2	MTFATHERCL	Mount Father Clancy	982	Continuous	Maalan	National Park	Tully Falls National Park	17°35'39.44"	145°36'55.53"	811	7.8.4a	3
15	1386C3	MAALANNP	Dirran (Maalan) Forest Reserve	611	Continuous	Maalan	National Park	Malaan National Park	17°35'36.71"	145°35'11.25"	890	7.8.4a	5
16	1386C4	BEATRICE	Beatrice	1353	Continuous	Beatrice	Freehold		17°33'6.87"	145°34'14.58"	975	7.8.4a	3

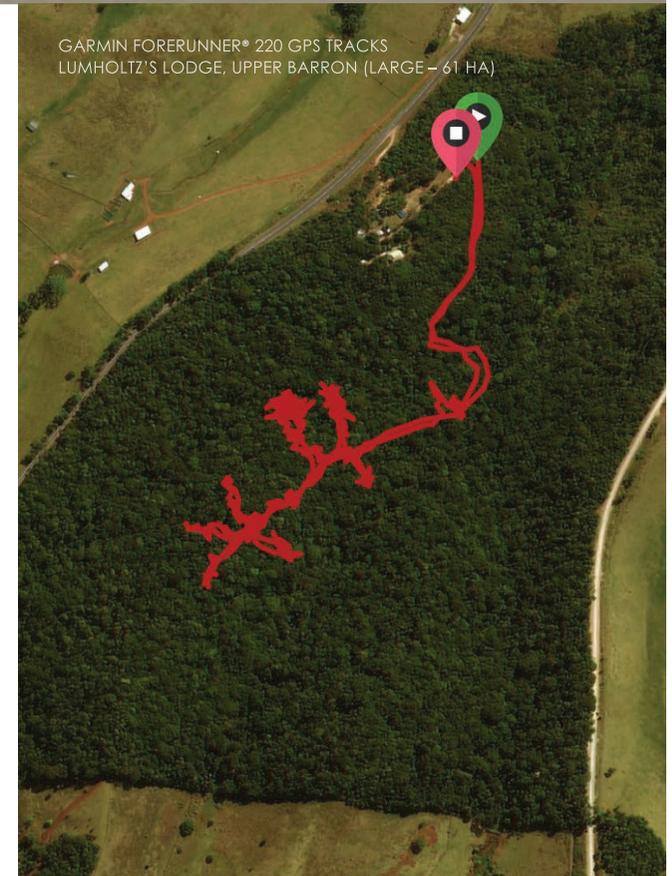
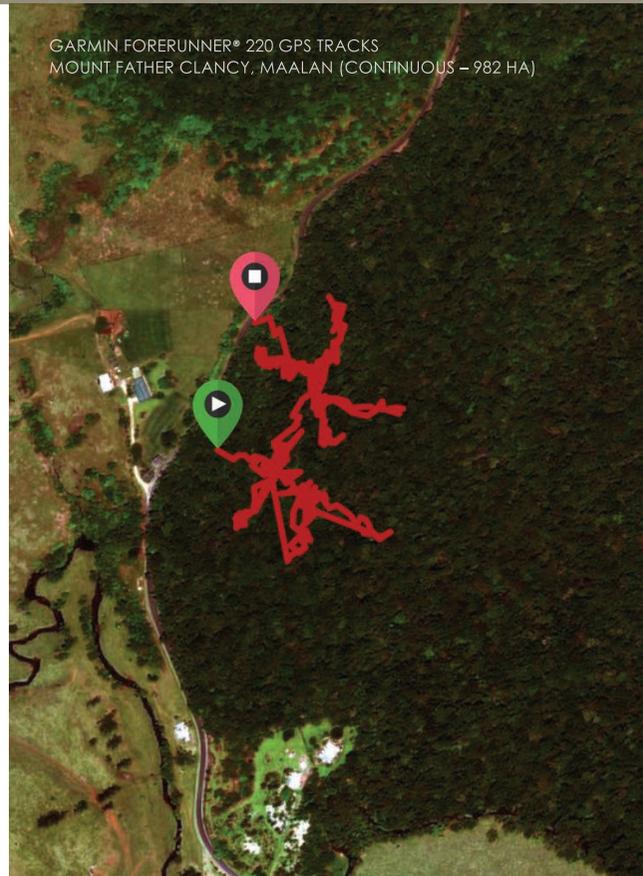
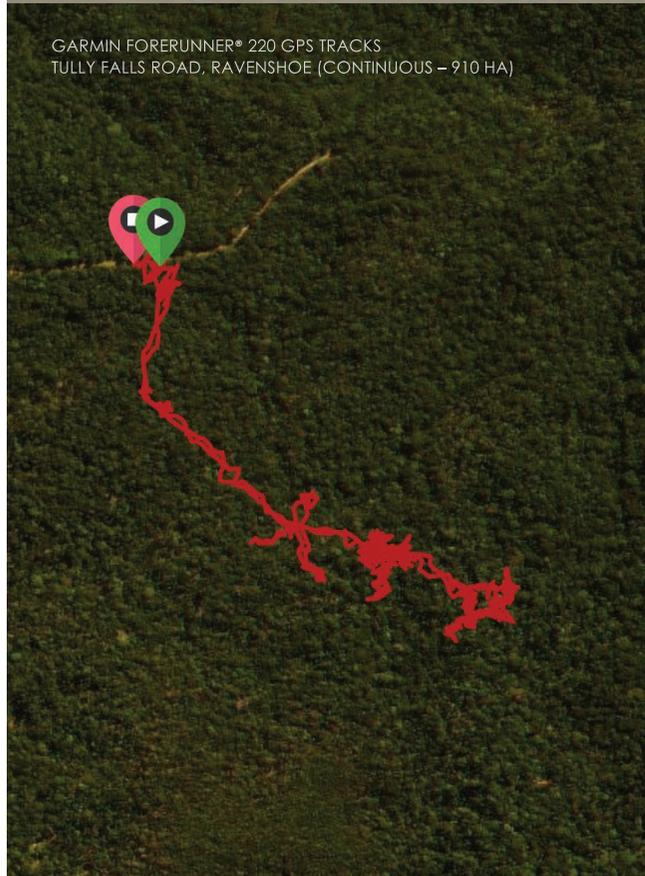
Four rainforest sites in each of four fragment-size classes were identified. Small remnants (<25 ha) (sites 1 – 4), medium remnants (26–50 ha) (sites 5 – 8), large remnants (>51 ha to 500 ha) (sites 9 – 12), and continuous rainforest (>501 ha) (sites 13–16) acting as reference for normal conditions. I then aimed to study the characteristics of at least 16 PYR territories in each fragment-size class (≥ 4 territories in each of the 16 sites, $n = \geq 64$) in a nested design. Sites were located on a mix of private land and protected areas.

APPENDIX B: Study sites map



The study area was located near Millaa Millaa ($17^{\circ}30'39.1''S$, $145^{\circ}36'50.2''E$) on the Atherton Tablelands, in Queensland's Wet Tropics. All sites were above 700 m ASL and classified as vegetation Type 5a (Tracey & CSIRO 1982), or 'Regional Ecosystem 7.8.4a' (DEHP 2017). This ecosystem is described as 'complex notophyll vine forest' and is found only on basaltic krasnozems in a very limited area of the cloudy-wet rainfall zone of the Wet Tropics. Its biodiversity status is listed as 'Endangered' (DEHP 2017). See also APPENDIX A: *Schedule of study sites*.

SURVEY AREA TRACKING



Upon entry into a site, a tracking session was begun on the Garmin Forerunner® 220 watch so that survey area could be estimated at a later stage. In order to calculate highly accurate population densities, I wanted to avoid extrapolating local area density data across whole fragment study sites. The total survey area at each site was determined by drawing a polygon with an approximately 30 m buffer on either side of the tracks. Upon completion of activity and exit from the site the Garmin Forerunner® 220 watch tracking session was concluded. These images were obtained from the Garmin Connect™ iPhone app (Garmin Australasia 2016).

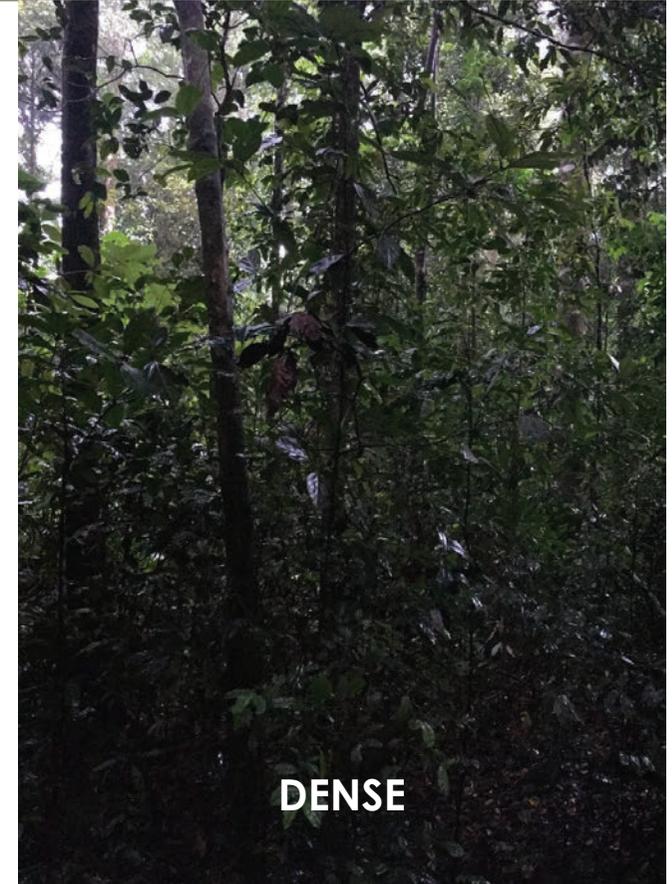
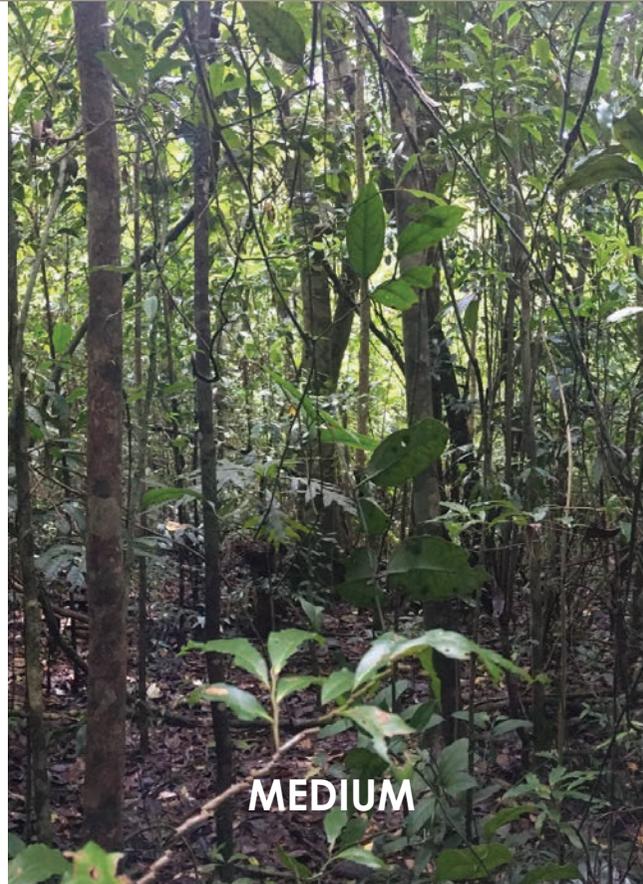
DATA VISUALISATION

L: BINNIE, UPPER BARRON (MEDIUM – 26 HA)
R: LUMHOLTZ'S LODGE, UPPER BARRON (LARGE – 61 HA)



GPS waypoints and tracking data were visualised in ArcGIS (ESRI 2011). RE 7.8.4 vegetation type is shown as light brown. Each territory (dark brown) was drawn as a polygon by connecting the 'end' waypoints by a straight line. The total survey area at each site was determined by drawing a polygon (yellow) with an approximately 30 m buffer on either side of the Garmin Forerunner® 220 tracks (yellow spots). Territories that were detected but not mapped were noted, and are represented above as white rings. These territories were counted in the population density 'territories per ha' calculations as long as they were >80% within the survey area.

UNDERSTORY <2 m DENSITY



For each habitat survey, 15 variables were measured: PYR presence / absence, canopy cover, understory (<2 m) density, stems per m², 'wait-a-while' (*Calamus* sp.) presence / absence, tree-falls, edge, gully, slope, coarse woody debris in three size categories, buttress roots, and leaf litter cover and depth. Understory (<2 m) density was visually assessed and described as either 'open', 'medium', or 'dense' using these three reference site photographs (Cornils et al 2015).