

Phylogeography and Conservation Biology
of the Purple-crowned Fairy-wren,
Malurus coronatus



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Illustration on previous page: John Gould (1804 – 1881)

DECLARATION

The work described in this thesis is my own original work and no part has previously been submitted for a degree or diploma at any university. Where others have contributed to this research they are duly acknowledged and are indicated at the beginning of each chapter. This work was carried out under permits from the Australian Bird and Bat Banding Scheme (2770), State governments (NT: 29948, WA: BB002411), and the Australian National University Ethics Committee (F.BTZ. 07.07).



Anja Skroblin

2/2/2012

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PREFACE

This thesis is structured as a series of manuscripts that have been or will be submitted to be published in scientific journals. With the exception of Chapter 1 (Introduction) and Chapter 7 (Conclusion), the content of the chapters is presented as it would appear in the relevant journal, with minor formatting differences. As the chapters are developed as stand-alone manuscripts for publication, some repetition between chapters was unavoidable. In the third chapter *Malurus coronatus coronatus* is referred to as vulnerable, however as the findings presented in this chapter resulted in an upgrade in the conservation status of the species, *M. c. coronatus* is identified as endangered in other data chapters. Chapter three was published in *Emu* in 2010 and is referred to as Skroblin *et al.* (2010), and chapter four was published in *Austral Ecology* in 2011 and is referred to as Skroblin *et al.* (2011) throughout the thesis. All other chapters are referenced by their chapter number. The vast majority of work contained within this thesis is my own. Other contributors to this research are listed as co-authors at the beginning of chapters, and their specific contributions are listed below. My supervisors Andrew Cockburn and Sarah Legge provided helpful advice on all manuscripts, they participated in verbal discussions, edited work, and provided general support. Robert Lanfear provided assistance to conduct the phylogenetic analysis outlined in Chapter 2.

ABSTRACT

The purple-crowned fairy-wren (*Malurus coronatus*) is a declining passerine that is restricted to the dense patches of vegetation that grow along waterways in the wet-dry tropics of northern Australia. The species is threatened by ongoing degradation of riparian habitat caused by the grazing and trampling of introduced herbivores, intense fires and weed incursion. Although the western subspecies (*Malurus coronatus coronatus*) has been listed as endangered, conservation has been hampered by poor information regarding its distribution and what factors influence its fine-scale occurrence. This thesis aims to rectify these knowledge gaps and produce recommendations for management goals that could improve the conservation of *M. c. coronatus*, its riparian habitat, and other vulnerable species within the habitat.

To validate the use of *M. c. coronatus* as a separate unit for conservation, we firstly affirmed the genetic and thus evolutionary distinctiveness of the morphologically defined subspecies of purple-crowned fairy-wren (*M. c. coronatus* and *Malurus coronatus macgillivrayi*). Because *M. c. coronatus* was of greater conservation concern it became the focus of the subsequent chapters. Extensive aerial and ground surveys, accompanied by an analysis of population genetics, revealed that *M. c. coronatus* occurs as six genetically divergent sub-populations on the Fitzroy, Durack, Drysdale, Isdell, Victoria and northern Pentecost catchments. The distribution of the species appears to be constrained by three factors: 1) fine-scale vegetation structure, 2) presence of threatening processes, and 3) the extent and spatial pattern of habitat across the landscape. The fine-scale probability of occurrence increased with increasing density of the mid-storey and increasing height of emergent trees, while the presence of potential threatening processes (cattle grazing, fire and weeds) were variously negatively correlated with decreased levels of these important habitat attributes. Suitable habitat for the species was extremely fragmented and widely dispersed along waterways in the Kimberley section of the species distribution. Suitable habitat occurred mainly on pastoral lands.

The on-going decline of the purple-crowned fairy-wren signals the need for a targeted approach to conservation management; we suggest a regional plan that outlines management recommendations that are tailored to the specific requirements of each sub-population. The most urgent conservation attention may be required in the smallest subpopulations on the Isdell and Pentecost catchments. These populations are best managed through exclusion of herbivores and careful, fine-scale fire management. Elsewhere however, large and diffuse populations may be better maintained using landscape-scale conservation measures. Although reserves play a vital role in ecosystem conservation, landscape-scale environmental management, undertaken across properties of varying tenure, may be vital to manage widely dispersed species such as the purple-crowned fairy-wren that occur at low density across vast landscapes.

TABLE OF CONTENTS

DECLARATION.....	I
ACKNOWLEDGMENTS	III
PREFACE.....	VII
ABSTRACT	IX
TABLE OF CONTENTS	XI
LIST OF TABLES	XV
LIST OF FIGURES	XVII
CHAPTER 1	1
INTRODUCTION.....	1
1.1. Background	3
1.2. The purple-crowned fairy-wren: an endangered riparian habitat specialist	4
1.2.1. Life history	4
1.2.2. Distribution.....	7
1.2.3. Status	8
1.4. Objective and aims	9
1.5. Thesis overview	10
CHAPTER 2	13
GENETIC ANALYSIS CONFIRMS THE EVOLUTIONARY DISTINCTIVENESS OF THE ENDANGERED WESTERN SUBSPECIES OF THE PURPLE-CROWNED FAIRY-WREN, <i>MALURUS CORONATUS CORONATUS</i>	13
2.1. Abstract	15
2.2. Introduction.....	15
2.3. Materials and Methods.....	18
2.3.1. Genetic sampling.....	18
2.3.2. DNA extraction, genotyping and sequencing	18
2.3.3. Sequence editing	21
2.3.4. Phylogenetic analysis	21
2.3.5. Population genetic analysis.....	22
2.3.6. Morphological sampling.....	23
2.3.7. Analysis of morphology	23
2.4. Results	24
2.4.1. Haplotype diversity	24
2.4.2. Phylogenetic analyses.....	26
2.4.3. Population genetics	27
2.4.4. Morphology	28

2.5. Discussion.....	30
2.5.1. Genetic divisions within <i>M. coronatus</i>	30
2.5.2. Connectivity within subspecies	32
2.5.3. Management directives	33
CHAPTER 3	35
THE DISTRIBUTION AND STATUS OF THE WESTERN SUBSPECIES OF THE PURPLE-CROWNED FAIRY-WREN (<i>MALURUS CORONATUS CORONATUS</i>).....	35
3.1. Abstract.....	37
3.2. Introduction	37
3.3. Methods.....	40
3.3.1. Study area	40
3.3.2. Study species	40
3.3.3. Collation of sightings	40
3.3.4. Survey design	42
3.3.4. Survey method	46
3.3.5. Social composition of groups	48
3.4. Results	48
3.4.1. Survey findings	48
3.5. Discussion.....	54
3.5.1. Current distribution	54
3.5.2. Population trends.....	55
3.5.3. Conservation directions	57
CHAPTER 4	59
THE INFLUENCE OF FINE-SCALE HABITAT REQUIREMENTS AND RIPARIAN DEGRADATION ON THE DISTRIBUTION OF THE PURPLE-CROWNED FAIRY- WREN (<i>MALURUS CORONATUS CORONATUS</i>) IN NORTHERN AUSTRALIA	59
4.1. Abstract.....	61
4.2. Introduction	62
4.3. Methods.....	64
4.3.1. Survey design	64
4.3.2. Survey method	64
4.3.3. Measurement of habitat attributes	65
4.3.4. Analysis of habitat requirements.....	67
4.3.5. Model validation	69
4.3.6. Prediction of habitat suitability	70
4.4. Results	71
4.4.1. Survey findings.....	71
4.4.2. Correlations between variates	73
4.4.3. Habitat requirements	73
4.5. Discussion.....	77
4.5.1. Fine-scale habitat requirements	77

4.5.2. Distribution of habitat types	78
4.5.3. Habitat degradation and population persistence	79
4.5.4. Unexplained variation in distribution	80
4.5.5. Implications	80
CHAPTER 5.....	83
UP THE CREEK WITHOUT A PADDLE: THE POPULATION GENETICS OF THE PURPLE-CROWNED FAIRY-WREN, A DECLINING RIPARIAN PASSERINE	83
5.1. Abstract	85
5.2. Introduction.....	85
5.3. Methods	87
5.3.1. Sampling design.....	87
5.3.2. DNA extraction and genotyping	89
5.3.3. Genetic diversity	90
5.3.4. Population Genetic structure.....	90
5.4. Results.....	91
5.4.1. Genetic diversity	91
5.4.2. Population genetic structure	93
5.5. Discussion	98
5.5.1. Population genetic structure	98
5.5.2. Small and isolated populations.....	99
5.5.3. Consequences of future degradation and fragmentation.....	101
CHAPTER 6.....	103
CONSERVATION OF A PATCHILY DISTRIBUTED AND DECLINING SPECIES ACROSS A VAST LANDSCAPE: THE NEED FOR A COLLABORATIVE LANDSCAPE-SCALE APPROACH	103
6.1. Abstract	105
6.2. Introduction.....	105
6.3. Methods	107
6.3.1. Survey design.....	107
6.3.2. Vegetation mapping.....	108
6.3.3. Vegetation attributes.....	110
6.3.4. Bird surveys	111
6.3.5. Statistical data analysis	112
6.3.6. Distribution of suitable habitat across land tenure types.....	113
6.3.7. Population estimates.....	114
6.4. Results.....	114
6.4.1. Survey findings	114
6.4.2. Model of habitat suitability.....	115
6.4.3. Distribution of suitable habitat.....	117
6.4.4. Population estimates.....	120

6.5. Discussion.....	121
6.5.1. <i>Determinants of distribution</i>	<i>122</i>
6.5.2. <i>Conservation approach – regional-scale.....</i>	<i>122</i>
6.5.3. <i>Management directives</i>	<i>123</i>
6.6. Conclusion.....	125
 CHAPTER 7	 127
SUMMARY AND FUTURE RESEARCH DIRECTIONS	127
7.1. Conclusion.....	129
 8. BIBLIOGRAPHY.....	 132
 9. APPENDIX	 149
AUSTRALIAN FRESHWATER CROCODILE (<i>CROCODYLUS JOHNSTONI</i>)	
ATTACKS ON HUMANS	149
A.1. Introduction	151
A.2. Methods	151
A.3. Results	152
A.4. Case Study.....	154
A.5. Discussion	156
A.6. Acknowledgments.....	158
A.7. Literature cited	158

LIST OF TABLES

Table 2.1. Geographical locations at which individuals used in phylogenetic analysis were sampled.....	20
Table 2.2. Partitioning of genetic variation within and among the Kimberley, Victoria and Gulf districts using AMOVA.....	27
Table 2.3. Pair-wise ϕ PT differences between the Kimberley, Victoria and Gulf districts using AMOVA.....	27
Table 3.1. Bird survey locations 2007 – 2009.....	44
Table 3.2. Summary of the survey for <i>M. c. coronatus</i> and the social composition of encountered territorial groups.....	49
Table 4.1. Description of fine-scale habitat attributes recorded at sites surveyed for the presence of the purple-crowned fairy-wren (N= 635).....	66
Table 4.2. Correlations between riparian habitat attributes for catchments where purple-crowned fairy-wrens have ever occurred.....	lxxii
Table 4.3. The importance of vegetation attributes in explaining the presence of the purple-crowned fairy-wren.....	74
Table 4.4. The importance of river structure in explaining the presence of the purple-crowned fairy-wren.....	74
Table 4.5. The importance of threatening process in explaining the presence of the purple-crowned fairy-wren.....	74
Table 4.6. The predictive model of the importance of habitat parameters for occurrence of the purple-crowned fairy-wren.....	75
Table 4.7. Results of the cross-validation procedure assessing the accuracy of the predictive model to predict occurrence of the purple-crowned fairy-wren.....	76
Table 5.1. Genetic diversity of seven microsatellite markers across six sub-populations of <i>M. c. coronatus</i>	92
Table 5.2. Partitioning of genetic variation within and among catchments using AMOVA.....	93
Table 5.3. Pairwise Φ PT differences between catchments calculated using AMOVA.....	94
Table 6.1. Sections of waterways surveyed in the Kimberley region for riparian vegetation suitable for the purple-crowned fairy-wren.....	109
Table 6.2. Vegetation attributes of patches recorded during aerial vegetation mapping.....	110
Table 6.3. Summary of the extent of riparian vegetation mapped during aerial surveys of 14 catchments within the Kimberley region.....	115
Table 6.4. Correlations between patch attributes for catchments within the current range of the purple-crowned fairy-wren.....	116
Table 6.5. Results of model selection using a multi-model inference framework for habitat suitability of riparian vegetation patches for the purple-crowned fairy-wren.....	116
Table 6.6. Model averaged coefficients, standard errors and weighting for each variable included in the 90% confidence set of models.....	116
Table 6.7. Estimates of the extent of suitable habitat and the resulting <i>theoretical</i> number of purple-crowned fairy-wrens and their territories that could occur on 14 catchments within the Kimberley region.....	121
Table A.1. Compiled accounts of <i>Crocodylus johnstoni</i> attacks on humans in northern Australia, 1971–2009.....	153

LIST OF FIGURES

Figure 1.1. A territorial pair of <i>M. c. coronatus</i> , the male with his purple-crown is below the female	5
Figure 1.2. <i>M. c. coronatus</i> territory with understorey dominated by <i>Pandanus aquaticus</i>	6
Figure 1.3. <i>M. c. coronatus</i> territory with understorey dominated by <i>Chionachne cyanthopoda</i>	6
Figure 1.4. The distribution of sightings of <i>M. coronatus</i> in the wet-dry tropics of Australia	7
Figure 1.5. The thirteen catchments on which <i>M. c. coronatus</i> has been estimated to occur, and catchments where the species occurrence has been confirmed.	8
Figure 2.1. The distribution of the purple-crowned fairy-wren with morphological and genetic sampling locations indicated.	19
Figure 2.2. Unrooted haplotype network of <i>Malurus coronatus</i> ND2 sequences.	25
Figure 2.3. The Maximum Likelihood (ML) tree of <i>Malurus coronatus</i> ND2 haplotypes.	26
Figure 2.4. Morphological variation of male and female purple-crowned fairy-wrens sampled from the Kimberley (Kimb), Victoria (Vic) and Gulf districts.	29
Figure. 3.1. Historical sightings of the western subspecies of Purple-crowned Fairy-wren across the range of the species.....	41
Figure 3.2. Locations surveyed for the western subspecies of Purple-crowned Fairy-wren during this study, 2007–09.....	43
Figure 3.3. The distribution of the western subspecies of Purple-crowned Fairy-wren (PCFW) in 2010.	50
Figure 3.4. Location of territories of the western subspecies of Purple-crowned Fairy-wren (PCFW) found during 2007–09 with respect to land tenure.....	53
Figure 4.1. Locations where fine-scale habitat attributes were quantified across the distribution of the western purple-crowned fairy-wren.	68
Figure 4.2. The relationship between the predicted occurrence and the distribution of the western purple-crowned fairy-wren.	76
Figure 5.1. Locations where <i>M. c. coronatus</i> was sampled for genotyping (N= 79).	88
Figure 5.2. Principal Coordinates Analysis of Φ_{PT} differences between catchment populations of purple-crowned fairy-wrens.	94
Figure 5.3. Relationship between pairwise Φ_{PT} values and geographical distance as measured in Euclidean distance between catchment populations. Mantel test of isolation by distance: $r = -0.31$, $P = 0.31$	95
Figure 5.4. Estimated number of genetic clusters of <i>M. c. coronatus</i> from Bayesian structure analysis using the program STRUCTURE 2.2.3.	96
Figure 5.5. Results of the Bayesian structure analysis using the program STRUCTURE 2.2.3.	97
Figure 6.1. Riparian vegetation mapped during helicopter surveys of waterways in the Kimberley region of Western Australia.....	111
Figure 6.2. The predicted extent of suitable habitat ($HS > 0.5$) for the purple-crowned fairy-wren across catchments in the Kimberley Region with respect to land tenure.	118
Figure 6.3. The predicted location of suitable riparian vegetation for the purple-crowned fairy-wren within the Kimberley region. Only rivers where the species now occurs or previously occurred but has since disappeared are indicated.	119
Figure. A.1. Hand and arm wounds from <i>Crocodylus johnstoni</i> less than an hour after attack.	155
Figure. A.2. Leg wounds from <i>Crocodylus johnstoni</i> five days after attack	155

CHAPTER 1

Introduction



Female purple-crowned fairy-wren

© Steve Murphy

“I think the present species is entitled to the palm for elegance and beauty, not only among the members of its own genus....but among all other birds yet discovered” John Gould (1865)

1.1. Background

Destruction, fragmentation and degradation of habitat are arguably the most important processes presently threatening species on a global level. Subdivision of populations within an increasingly fragmented landscape often results in negative impacts on the demography and genetic diversity of populations, and these may increase both the short and long term extinction risk of threatened species (Lande 1988; Holsinger 2000; Spielman *et al.* 2004). Understanding the processes occurring in fragmented populations, such as the subdivision of populations (Allendorf and Luikart 2007), disrupted dispersal (Hoehn *et al.* 2007; Coulon *et al.* 2010), increased genetic drift and inbreeding (Frankham 1996) and their consequences on population viability and fitness (Frankham *et al.* 2002; Athrey *et al.* 2011), is critical to improve conservation management outcomes for threatened species.

Many riparian ecosystems are being threatened by human-induced land modification and degradation. Riparian areas are of critical conservation concern as they often support a high species richness within both their aquatic and terrestrial components (Naiman *et al.* 1993; Sabo *et al.* 2005), and are experiencing a range of threats (Bren 1993; Belsky *et al.* 1999; Scott *et al.* 2003). In northern Australia, riparian habitats are generally more productive than the surrounding savannah-woodland habitats (Russell-Smith 1991; Woinarski *et al.* 2000) and support a diverse range of taxa, including a particularly rich avifauna (Woinarski *et al.* 2000). Unfortunately, the quality of riparian habitat in northern Australia is declining (National Land and Resources Audit 2002).

Riparian vegetation is being degraded over large parts of the tropics by intense fires (Woinarski 1990; Russell-Smith *et al.* 2003; Valentine *et al.* 2007), weed incursion, and grazing by introduced herbivores (Rowley 1993; McKenzie *et al.* 2009). Although the ecological impact of this decline is undoubtedly extensive, conservation management of riparian habitat in northern Australia has gained limited attention (Woinarski *et al.* 2000). Conservation that is targeted to improve the persistence of riparian endemics could have broad benefits for the health of riparian areas and the species that utilize these areas.

1.2. The purple-crowned fairy-wren: an endangered riparian habitat specialist

In this thesis I investigate topics relevant to improving the conservation management of a riparian habitat specialist: the purple-crowned fairy-wren (*Malurus coronatus*). This species is restricted to the dense vegetation that naturally occurs as discrete patches along the waterways of northern Australia. It has suffered declines in distribution and density as a result of riparian degradation that has been occurring since the advent of pastoralism during the early 20th century. The western subspecies, *M. c. coronatus*, has been particularly affected. It is listed as vulnerable nationally (*Environment Protection & Biodiversity Conservation Act 1999* (Aust.)) on the basis of declines in both population density and distribution (DEWHA 2009). It is listed as Endangered within the Action Plan for Australian Birds (Garnett *et. al.* 2011) based on a series of studies (Rowley 1993; van Doorn 2007; Skroblin and Legge 2010) that have revealed continuing contraction and deterioration in the quality of riparian habitat, as well as declines in the area of occupancy, number of locations, subpopulations and mature individuals. The Action Plan for Australian Birds provides conservation advice, whilst legislative protection is conferred under the *EPBC Act 1999*.

Conservation of the purple-crowned fairy-wren however, has been hampered by poor information regarding its distribution, and how that distribution is influenced by the quality of riparian habitat and the threatening processes that are occurring across its range. The aim of this study is to rectify these knowledge gaps, and in particular investigate the factors that influence the persistence of this riparian habitat specialist. Below, I briefly describe the life history of the species and what is known about its distribution and decline.

1.2.1. Life history

The purple-crowned fairy-wren is the largest of 13 species in the genus *Malurus*, which is confined to Australia and Papua New Guinea (Rowley and Russell 1997). The species achieves its name from the distinctive purple circle of crown feathers sported by breeding males (Figure 1.1). Like all other *Malurus*, the purple-crowned fairy-wren is a cooperative breeder (Rowley

and Russell 1993; van Doorn 2007; Kingma *et al.* 2010), and lives in sedentary groups that maintain their territories year-round. However unlike other species in the genus, it is highly faithful and displays low rates of extra-pair paternity (Kingma *et al.* 2009). Groups generally comprise of a breeding pair that is helped by one to six offspring from previous broods, and helpers may stay with their parents for several years before attempting to breed (Rowley and Russell 1993; van Doorn 2007; Kingma *et al.* 2010). Most dispersal occurs when helpers abandon their natal territories in search of their own breeding territory. Males generally disperse shorter distances than females (Rowley and Russell 1993), and the species has not been observed at great distances away from riparian habitat.



Figure 1.1. A territorial pair of *M. c. coronatus*, the male with his purple-crown is below the female. © Michelle Hall

The spatial arrangement of purple-crowned fairy-wren territories differs with what plant species dominate the understorey. In areas where the understorey is dominated by *Pandanus aquaticus* (a palm-like shrub that grows in dense, narrow-stands on the immediate edge of watercourses; Figure 1.2), territories are arranged in a linear fashion, and generally occupy between 50-300m of river length (Rowley and Russell 1993; Kingma *et al.* 2009). Territories may be arranged in a mosaic pattern where the understorey is comprised by tall river-grasses (in

particular *Chionachne cyanthopoda*; Figure 1.3). These grasses often grow as vast swathes, sometimes hundreds of meters wide along riverbanks (van Doorn and Low Choy 2009).

Breeding can occur at any time of the year with peaks in the early and late dry season (March – May and August – November) (Rowley and Russell 1993; van Doorn 2007). Nests are built mainly of fine rootlets, grass, leaves and strips of bark. Incubation of clutches comprising 2-3 eggs occurs for 14 days, and chicks fledge after 10 days (Rowley and Russell 1993). The species is mainly insectivorous, and consumes a range of small invertebrates.



Figure 1.2. *M. c. coronatus* territory with understorey dominated by *Pandanus aquaticus*



Figure 1.3. *M. c. coronatus* territory with understorey dominated by *Chionachne cyanthopoda*

1.2.2. Distribution

The purple-crowned fairy-wren has an extensive distribution across the wet-dry tropics of northern Australia (Figure 1.4). The species' distribution spans more than 1500km, and includes rivers in the Kimberley region of Western Australia, and the Victoria River District in the Northern Territory, as well as, rivers that drain into the western edge of the Gulf of Carpentaria (Barrett *et. al.* 2003). Two sub-species are recognized: the western form (*Malurus coronatus coronatus*) occurs in the Kimberley and Victoria River regions, while the eastern form (*Malurus coronatus macgillivrayi*) occurs on the rivers along the Gulf of Carpentaria (Schodde 1982). The two subspecies are separated by approximately 300km of semi-arid uplands that contain few waterways and thus no suitable habitat, and have been split based on differences in plumage colouration and body size of museum skins: the western race is slightly larger and has a browner back, as well as a buff-coloured, rather than white, breast and belly (Rowley and Russell 1997). The level of genetic divergence between the phenotypic subspecies has not been examined.

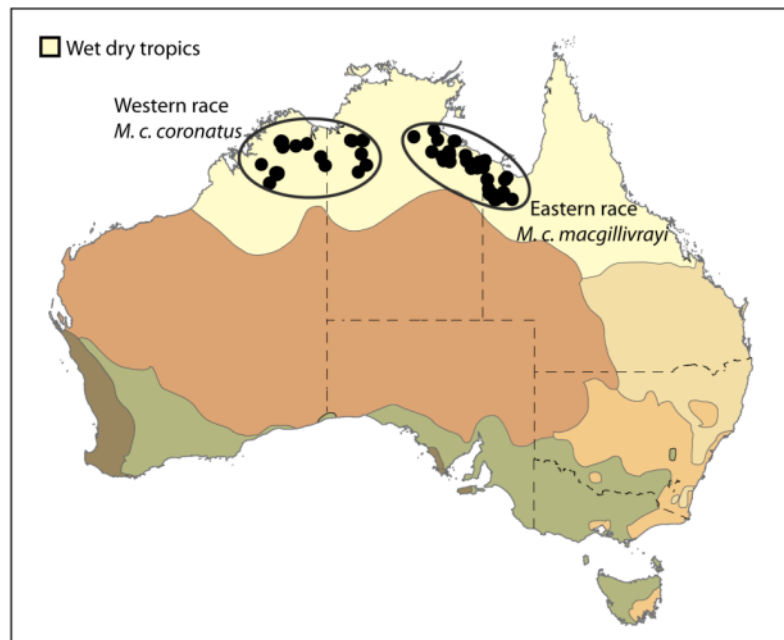


Figure 1.4. The distribution of sightings of *M. coronatus* in the wet-dry tropics of Australia (Barrett *et al.* 2003).

1.2.3. Status

Concern for the status of *M. c. coronatus* has been expressed since declines (Smith and Johnstone 1977), and the negative impact of habitat degradation (Boekel 1979), were first reported several decades ago. These reports prompted a review of the recent history of *M. coronatus*: the current distribution, locations of decline and status (Rowley 1993). Although population trends were well documented for areas that were visited often, the overall distribution of the species remained poorly known because many rivers within the species range are extremely inaccessible. The federal species profile for *M. coronatus* (DEWHA 2009), based on multiple descriptions of distribution (Aumann 1991; Rowley 1993; Johnstone and Storr 2004), estimated that 13 isolated subpopulations of *M. coronatus* occurred on 13 different catchments (Figure 1.5). However, sightings of the species had only been confirmed on seven of these catchments: the Fitzroy, Isdell, Durack, Pentecost, Victoria, Drysdale and Ord (Rowley 1993; Barrett *et al.* 2003). The distribution of the species on the other six catchments has been inferred based on unconfirmed sightings and the likelihood that suitable habitat may occur (Rowley 1993).

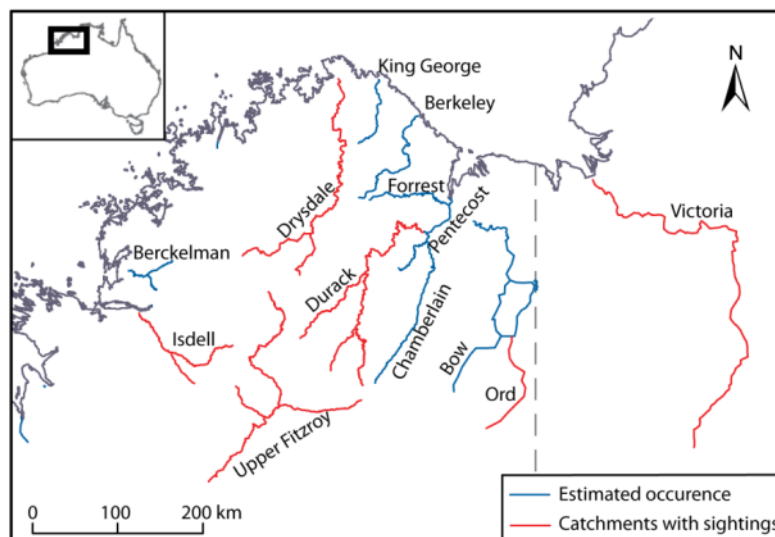


Figure 1.5. The thirteen catchments on which *M. c. coronatus* has been estimated to occur, and catchments where the species occurrence has been confirmed.

Due to a paucity of information, estimates of the size and location of remnant populations were of low reliability (Garnett and Crowley 2000). In addition, no information was available on the connectivity of fairy-wren populations that occur on separate catchments, or the extent to which remnant populations were impacted on by continuing degradation. Clearly, further research is required to identify the locations of subpopulations and assess their likelihood of persistence before appropriate actions to conserve *M. c. coronatus* can be developed.

1.4. Objective and aims

In this thesis I use several approaches: on-ground surveys, predictive habitat modelling and genetic analyses, to examine the distribution, habitat associations and population structure of the purple-crowned fairy-wren. This knowledge is applied to form recommendations for land management that would improve the conservation of the purple-crowned fairy-wren, its riparian habitat and other similarly vulnerable communities.

The specific aims of this study were to:

- 1) Investigate the genetic basis of subspecies division in *M. coronatus*
- 2) Comprehensively survey the distribution of *M. c. coronatus*
- 3) Investigate the effects of habitat degradation on species occurrence
- 4) Assess the quality and amount of habitat available to the species
- 5) Define subpopulation boundaries and estimate the size and probability of persistence
- 6) Develop specific conservation recommendations

1.5. Thesis overview

This thesis consists of seven discrete chapters. This brief introductory chapter is followed by five data chapters, a concluding chapter and an appendix. The first data chapter (Chapter 2) examines whether the two subspecies of purple-crowned fairy-wren: *M. c. macgillivrayi* and *M. c. coronatus*, which were defined based on morphological differences in museum specimens (Schodde 1982), represent distinct genetic groups. This investigation was undertaken by analysing mitochondrial DNA sequences and morphological measurements from individuals that were sampled from across the species range. The understanding of the genetic distinctiveness of these subspecies will help guide management to conserve important evolutionary and ecological processes occurring within populations of *M. c. coronatus*.

The third chapter presents the first comprehensive survey of the distribution of purple-crowned fairy-wrens in the Kimberley region. It compares the findings of this survey with a dataset of historical records to describe population trends and identify priority areas for conservation intervention. Chapter 3 provides essential information for the development of the subsequent chapters.

In the fourth chapter I investigate how fine-scale habitat requirements and riparian degradation influence the distribution of *M. c. coronatus*. This chapter describes the habitat requirements of the species and investigates the processes that constrain distribution. By identifying threatening processes, this chapter outlines management actions that would maintain or enhance the quality of riparian habitat. The habitat associations described in this chapter are moreover used to establish the habitat mapping method utilized in Chapter 6.

The fifth chapter outlines the population genetic structure of *M. c. coronatus*. The chapter documents the results of two analytical methods to identify subpopulation boundaries and dispersal patterns from multi-locus microsatellite data. By identifying barriers to dispersal and population boundaries, this chapter describes how habitat degradation has impacted on connectivity across the species' range and discusses the likely threats to persistence of subpopulations.

In Chapter 6, I use information on the distribution of *M. c. coronatus* (Chapter 2) and its habitat requirements (Chapter 4) to develop a procedure for mapping the extent and location of riparian vegetation that could be suitable habitat for the species. I use information on population boundaries (Chapter 5) to estimate the size of subpopulations and variation in threatening processes between populations. This data is vital to guide the region-wide conservation management of the species.

The final chapter (Chapter 7) provides a brief synthesis of the main findings of earlier chapters and outlines suggestions for further research. The main part of thesis is followed by an Appendix which reviews attacks of the freshwater crocodile (*Crocodylus johnstoni*) on humans. Although the topic of the Appendix is not directly related to the thesis, it describes research which resulted from experiences that occurred while undertaking the field work for this thesis.

CHAPTER 2

Genetic analysis confirms the evolutionary distinctiveness of the endangered western subspecies of the purple-crowned fairy-wren, *Malurus coronatus* *coronatus*

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Breeding male *M. c. coronatus*

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2.1. Abstract

Conservation managers require knowledge of population structure and connectivity to implement effective conservation measures for threatened species. We analysed mitochondrial DNA sequences from 87 purple-crowned fairy-wrens (*Malurus coronatus*) to identify barriers to dispersal across the distribution of *M. coronatus*, and propose conservation actions that maintain natural patterns of gene flow. Our analysis identified phylogenetic clusters that correspond with the morphologically defined eastern (*M. c. coronatus*) and western taxonomic (*M. c. macgillivrayi*) division of the species. The genetic divergence between these subspecies is consistent with their isolation by a natural barrier to gene flow, and verifies their independent conservation management. The lack of genetic structure within each of the two subspecies indicates that females are capable of both long-distance and between-catchment dispersal, whereas the slight morphological divergence between *M. c. coronatus* in the Kimberley and Victoria River districts suggest that these areas may contain separate subpopulations linked by gene-flow. It is likely that these natural patterns of connectivity have been disrupted by widespread habitat degradation that threatens the Endangered *M. c. coronatus*. Conservation of *M. coronatus* must preserve quality habitat and restore connectivity between isolated populations to prevent further population declines.

2.2. Introduction

Conservation managers require knowledge of population structure to implement effective conservation measures for threatened species (Thrall *et. al.* 2000; Segelbacher *et. al.* 2010). This information can be used to identify populations that warrant separate management (Paetkau 1999; Palsboll *et. al.* 2007), prioritize conservation actions (McDonald-Madden *et. al.* 2008), and enhance restoration, translocation, and captive-breeding programs (Montgomery *et. al.* 1997; Moritz 1999). Furthermore, maintaining population structure within threatened species may allow preservation of their evolutionary potential (Crandall *et. al.* 2000; Moritz 2002).

Knowledge of population genetic structure is required to aid conservation management of the purple-crowned fairy-wren *Malurus coronatus*. The purple-crowned fairy-wren is a riparian habitat specialist that occurs in patches of dense river-fringing vegetation in northern Australia (Figure 1.4). The species has declined across parts of its range and is threatened by the degradation and fragmentation of riparian vegetation caused by the grazing of introduced herbivores, weed incursion and repeated intense fires (Smith & Johnstone 1977; Rowley & Russell 1993; Garnett et al. 2011; Skroblin & Legge 2011). Conservation initiatives have been suggested to halt population declines and restore connectivity (Rowley 1993; Skroblin and Legge 2010; Skroblin and Legge 2011; van Doorn 2007). However, an understanding of pre-degradation population structure is required to ensure that management actions, if possible, enhance natural patterns of gene flow and maintain any adaptive divergence between populations (Moritz 1994; Crandall *et al.* 2000).

Two subspecies of the purple-crowned fairy-wren are recognized (Schodde 1982; Higgins *et al.* 2001), and receive separate conservation management listings (Garnett *et al.* 2011). The eastern form, *M. c. macgillivrayi* occurring in the Gulf of Carpentaria, is considered to be Near Threatened (Garnett *et al.* 2011), although population dynamics are unknown. By contrast, the western form, *M. c. coronatus* occurring in the Kimberley and Victoria River, is listed as Vulnerable nationally (*Environment Protection & Biodiversity Conservation Act 1999 (Aust.)*) (DEWHA 2009), but has recently been described as Endangered (Garnett *et al.* 2011) on the basis of a series of studies revealing declines in its distribution (Rowley 1993; van Doorn 2007; Skroblin and Legge 2010). The two subspecies are separated by a natural break of approximately 300km of unsuitable habitat (Rowley 1993), and have been split based on differences in plumage colouration and body size of museum skins (Schodde 1982; Higgins *et al.* 2001). Although subspecies that are defined by phenotypic differences are often used as units for conservation management, their use could misdirect conservation effort if they represent geographic divisions of character clines that are weakly associated with underlying genetic diversity (Avice *et al.* 1987; Zink 2004; Remsen 2005; Rising *et al.* 2009). The

conservation of the purple-crowned fairy-wren may therefore benefit from genetic analysis to assess the appropriateness of the phenotypically delineated subspecies, and therefore their separate conservation rankings, as well as identify any further population divisions that were not evident in previous analyses of morphology (Zink 2004; Phillimore and Owens 2006).

Without an understanding of historical connectivity across the range of *M. coronatus*, it is difficult to gauge the effect anthropogenic degradation of riparian habitat (occurring since the early 20th century) has had on population dynamics, and hence determine appropriate management strategies. Observations of limited flight capabilities and a strong adherence to dense river-fringing vegetation (Rowley and Russell 1993), suggest that the species has a limited potential for dispersal between widely-spaced waterways or patches of isolated habitat (Rowley 1993). Of particular interest is the impact that the recent disappearance of purple-crowned fairy-wrens from the Ord River system, previously the centre of the range of *M. c. coronatus* (Skroblin and Legge 2010), will have on extant populations in the western Kimberley and Victoria River. The impact of this decline may be limited if movement between the western Kimberley and Victoria River was historically restricted by biogeographical barriers that have been found to separate populations of other terrestrial and aquatic species within the vicinity of the Ord River region (Unmack 2001; Bowman *et. al.* 2010; Fujita *et. al.* 2010; Melville *et. al.* 2011; Potter *et. al.* 2012). Conservation strategies for extant populations of *M. c. coronatus*, such as restoring connectivity, should be informed by the natural connectivity between remnant populations.

Here we investigate the broad-scale population structure of *M. coronatus* to aid in determining management priorities and strategies for effective conservation. We first employ phylogenetic analyses (Bayesian, maximum likelihood and statistical parsimony) to describe genetic structure and identify any phylogeographic clusters of individuals across the species range. We thereby aim to identify natural barriers to dispersal across the distribution of *M. coronatus*, and gain an understanding of how populations were connected prior to the habitat degradation that has occurred within the past 150 years (Rowley 1993; National Land and

Resources Audit 2002). We specifically test the hypothesis that the phenotypic subspecies of *M. coronatus* represent distinct evolutionary lineages, thereby verifying the appropriateness of delineation between populations in the Kimberley and Victoria Districts (*M. c. coronatus*) versus those in the Gulf (*M. c. macgillivrayi*) for conservation purposes. Finally, we use both genetic and morphological data to investigate the impact that the recent extirpation of purple-crowned fairy-wrens from the Ord River system, in the centre of the distribution of *M. c. coronatus*, may have on population dynamics within the subspecies. The similarity of fairy-wrens (both morphologically and genetically) in the western Kimberley with those on the Victoria River will increase understanding of historical connectivity and may inform whether potential actions to restore connectivity or translocations between these areas would be appropriate. An understanding of population structure within *M. coronatus* will allow managers to implement actions which conserve natural patterns of connectivity between populations and their evolutionary potential.

2.3. Materials and Methods

2.3.1. Genetic sampling

Blood samples were attained from 87 live purple-crowned fairy-wrens from throughout the three districts where the species occurs: Victoria (N = 29), Kimberley (N = 19), and Gulf (N = 39). Sampling effort was designed to maximise genetic variation (Figure 2.1). Samples were collected from purple-crowned fairy-wrens on seven rivers in the Kimberley, from three sites on the Victoria River (each separated by approximately 100 km of river distance) and on six rivers in the Gulf (Table 2.1). Only one individual per territorial group was sampled.

2.3.2. DNA extraction, genotyping and sequencing

DNA was extracted from blood samples using a conventional proteinase K, ammonium acetate and ethanol protocol. The approximate concentration of DNA was determined by electrophoresis in a 2% agarose gel stained with 160 ng / L ethidium bromide and visualized

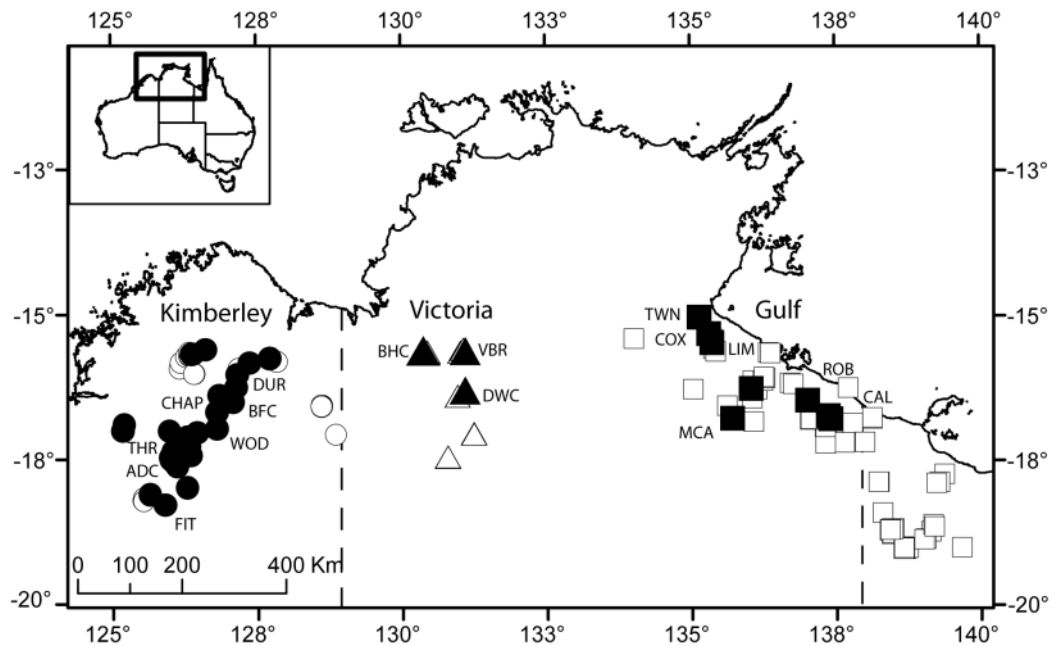


Figure 2.1. The distribution of the purple-crowned fairy-wren with morphological and genetic sampling locations indicated. Three districts are indicated: ○) Kimberley, △) Victoria River, and □) Gulf. Open symbols represent locations where the species has been sighted since 1996 (Skroblin and Legge 2010). The species is considered to occur at these localities except for the Ord River in the Kimberley where it has recently disappeared. Black symbols represent locations where morphology was measured. Genetic samples were also collected at sites labelled using three letter codes (Table 2.1).

under UV light. The NADH dehydrogenase subunit 2 (ND2) mitochondrial gene was sequenced for use in all genetic analyses. Although there are recognized drawbacks to using only mtDNA for genetic analysis (Funk and Omland 2003; Ballard and Whitlock 2004), the marker is highly appropriate for detecting patterns of recent evolution or isolation of the sort anticipated to occur in the purple-crowned fairy-wren (Rubinoff and Holland 2005; Zink and Barrowclough 2008; Zink 2010). The suitability of mtDNA for investigating recent phylogeographical divergence is due to its smaller effective population size and faster rate of molecular evolution than nuclear DNA (Avise *et al.* 1987; Moritz *et al.* 1987), which leads to both shorter coalescence times and higher diversity (Zink and Barrowclough 2008). The ND2 region was amplified with the primers L5215 (5'-TATCGGGCCCATACCCCGA AAAT-3'), (Hackett 1996) and H6313 (5'-

ACTCTTRTTTAAGGCTTTGAAGGC-3') (Sorenson *et. al.* 1999). The expected size of the amplified product was approximately 1000 bp. PCR products were purified by ammonium acetate (4M) and ethanol (100%) precipitation. Cycle-sequencing reactions contained 0.75 µL of BigDye (Applied Biosystems), 3 µL of 5x buffer, 0.32 µL of primer, 14.05 µL of doubly distilled water and 2 µL of purified PCR product. Cycle-sequencing consisted of 25 cycles at 94°C (5 s), 50°C (10 s) and 60°C (4 min). The product was precipitated using sodium acetate and ethanol. The pelleted DNA was washed three times in 70% ethanol. DNA pellets were dried before addition of 20 µL of HiDi formamide and sequencing on an ABI 3100 autosequencer (Applied Biosystems).

Table 2.1. Geographical locations at which individuals used in phylogenetic analysis were sampled.

The first letter in the *M. coronatus* sample codes represent the district from which the birds were sampled (G = Gulf; K = Kimberley; V= Victoria River). The site ID represents the river from which the birds were sampled.

Site name	N	Sample code	Site ID	Latitude (°S)	Longitude (°E)
<i>M. coronatus coronatus</i>	48				
Kimberley					
Wood River	1	K1	WOD	16.96	126.85
Chapman River	3	K2, K3, K4	CHAP	16.51	126.67
Blackfellow Creek	2	K5, K6	BFC	16.68	126.85
Fitzroy River	3	K7, K8, K19	FIT	17.43	126.39
Throssell River	3	K9, K10, K11	THR	17.45	126.05
Adcock River	1	K12	ADC	17.47	126.02
Durack River	6	K13 - K18	DUR	16.25	127.18
Victoria River					
Big Horse Creek	9	V1 - V9	BHC	15.62	130.42
Victoria River Crossing	8	V22 - V29	VBR	15.62	131.13
Dashwood Crossing	12	V10 - V21	DWC	16.33	131.11
<i>M. coronatus macgillivrayi</i>	39				
Gulf					
Limmen	2	G1, G2	LIM	15.48	135.39
Towns River	9	G3 - G11	TWN	15.04	135.18
Cox River	10	G12 - G21	COX	15.32	135.34
Calvert River	12	G22 - G33	CAL	16.73	137.41
Robinson River	2	G34, G35	ROB	16.46	137.05
McArthur River	4	G36 - G39	MCA	16.78	135.75

2.3.3. Sequence editing

Phylogenetic analyses were conducted to describe genetic structure and identify any phylogeographic clusters of individuals across the species range. Un-rooted genealogical relationships between sequences were estimated using statistical parsimony in TCS 1.21 (Clement *et. al.* 2000). Each haplotype was given a code (Figure 2.2.) and included once in subsequent phylogenetic analyses. For outgroup taxa in phylogenetic analyses, we included all 11 *Malurus* species that had ND2 sequences available in GenBank: *M. lamberti* (AY488326), *M. cyaneus* (EU534191), *M. splendens* (EU144301), *M. alboscapulatus* (JN598704), *M. amabilis* (JN614694), *M. elegans* (GU825876), *M. grayi* (JN598688), *M. leucopterus* (GU825875), *M. melanocephalus* (GU825874), *M. cyanocephalus* (JN598690), and *M. pulcherrimus* (JQ027484). The dataset was aligned using Geneious Pro 4.6.4 (Drummond *et. al.* 2010).

2.3.4. Phylogenetic analysis

PartitionFinder (Lanfear *et. al.* 2012) was used to choose the most appropriate partitioning scheme and the most appropriate model of DNA sequence evolution for each partition. To do this, we defined each codon position in ND2 as an initial data block, and performed an exhaustive search of all possible partitioning schemes ('search = all'), using the models of molecular evolution implemented in MrBayes 3.1.2 ('models = MrBayes'), and using the Bayesian Information Criterion ('model_selection = BIC') to choose partitioning schemes and models of molecular evolution. This method compares all possible combinations of codon positions to find the partitioning scheme and models of molecular evolution that are most appropriate for the data. The optimal partitioning scheme was to treat each codon position separately, using an HKY+G model for the first codon position, an HKY+I model for the second codon position, and a GTR model for the third codon position.

Bayesian phylogenetic analyses were performed using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001), with the partitioning scheme and models of molecular evolution selected in

PartitionFinder. The Bayesian Markov Chain Monte Carlo (MCMC) search was started with random trees and run for 100 million generations using one cold and three heated chains across two independent runs. Samples were taken from the MCMC every 10,000 generations and Tracer v1.5 (Rambaut and Drummond 2007) was used to check for stationarity of results. As calculation of posterior probabilities can be influenced by the starting point of the MCMC (Ronquist *et. al.* 2009) the first 1,000,000 generations of the analysis were discarded as burn-in. We used Tracer to check that the effective sample sizes of all parameters was sufficient (i.e. >200).

In addition to the Bayesian analyses, we conducted maximum likelihood (ML) phylogenetic analyses using RaxML v7.2 (Stamatakis 2006). ML analyses were conducted using the partitioning scheme selected in PartitionFinder, with a separate GTR+G model of molecular evolution applied to each partition. The ML tree was calculated using 100 search replicates, with 1,000 bootstrap replicates performed on re-sampled datasets (Figure 2.3).

2.3.5. Population genetic analysis

We used population genetic analyses to investigate the likely impact that the recent extirpation of purple-crowned fairy-wrens on the Ord River system (Skroblin and Legge 2010) may have on connectivity between remnant populations. For this analysis we partition the distribution of *M. coronatus* into three districts: the western Kimberley and Victoria River populations of *M. c. coronatus*, and the Gulf populations of *M. c. macgillivrayi*. We included these three districts in our analyses as the Victoria river population is now similarly isolated from the Gulf populations of *M. c. macgillivrayi* as it is from *M. c. coronatus* in the western Kimberley. We used sequences from all 87 individuals in an analysis of molecular variance (AMOVA; (Excoffier *et. al.* 1992)) to estimate partitioning of variance between populations in the three districts. AMOVA was implemented with 999 permutations for significance testing in GenAlEx 6.4. (Peakall and Smouse 2006). Pairwise Φ_{PT} values (fraction of the total variance that is among districts) were calculated to estimate divergence between the three districts.

2.3.6. *Morphological sampling*

Morphological measures were taken from purple-crowned fairy-wrens at a total of 41 sites across the three districts (Figure 2.1). In the Kimberley region, 159 males and 129 females were sampled from 30 sites across five catchments. In the Victoria River district, 34 males and 18 females were sampled from three sites, whereas in the Gulf, 51 males and 41 females were measured at eight sites across six rivers. Sex of birds was determined by plumage. Vernier callipers were used to measure, to the nearest 0.1 mm, tarsus length, head-bill length (from the back of the skull to the tip of the beak) and bill length. Weight was measured to the nearest 0.1 g using a spring-loaded Pesola balance, and a butted ruler was used to measure tail length and wing length (maximum chord). To avoid pseudo-replication, morphological traits were averaged for individuals of the same sex within a territory. The final dataset consisted of average body measurements from 188 male and 163 female territories. We tested for normality, homogeneity of variances and multicollinearity (correlation between independent traits) before commencement of analysis using GenStat 11.1 (VSN International).

2.3.7. *Analysis of morphology*

Multivariate analysis of variance (MANOVA) was performed to test for an effect of district on overall morphology of each sex, using a Wilks' Lambda test to investigate significance of among-district differences. Morphology may vary in response to latitudinal changes (Meiri and Dayan 2003). Therefore before morphology was compared between districts, a confounding effect of latitude was tested for, for each separate morphological trait in each sex using analysis of covariance (ANCOVA). Latitudinal effects were tested for in two ways. Firstly, as the three districts from which birds were sampled (Kimberley, Victoria, Gulf) differed significantly in latitude (ANOVA $F_{2,185} = 58$, $p < 0.001$), we examined the effect of latitude on the common-slope of each morphological trait across the districts. Secondly, as birds were sampled from territories occurring over a large latitudinal range (-15.61 to -18.29 Decimal Degrees), we tested for differential effects of latitude on each morphological trait within a district. In both cases a

covariate of latitude was used in ANCOVA. To assess whether trait morphology varied across the three districts we employed three methods dependant on whether an effect of latitude on the trait was evident: 1) ANOVA was used when no effect of latitude was evident, 2) Linear Models, with latitude as a covariate, were used if an effect of latitude was evident on the common-slope of the trait, and 3) ANCOVA, with latitude as the covariate, was employed if the effect of latitude varied between districts. All analyses were grouped by district (as the independent level of replication) and site nested within district.

2.4. Results

Partial ND2 sequences (960 bp) were obtained for 87 individuals. Base frequencies were representative of avian mitochondrial DNA (A = 0.29, T = 0.25, G = 0.10, C = 0.34) (Joseph and Wilke 2006; Kearns *et. al.* 2009). Neither multiple peaks nor mismatch in overlapping sequences were found. Translation into amino acids did not reveal any internal stop codons and tests for neutrality were not significant. This suggests the sequences were mitochondrial in origin rather than nuclear copies (numts) of ND2 sequences (Zhang and Hewitt 1996; Sorenson and Quinn 1998).

2.4.1. Haplotype diversity

The two subspecies of *M. coronatus* were each found to contain a unique set of ND2 haplotypes that were separated by eight mutational steps (Figure 2.2). A total of 16 haplotypes were contained within the 87 individuals sampled, and haplotype diversity was similar for the eastern and western populations. The eastern polytomy ($N = 38$; 8 haplotypes) contained shallow genetic structure (Figure 2.2). Two internal haplotypes (separated by two mutational steps) were common and each shared by 13 individuals. The three haplotypes radiating from each of internal haplotype were no more than two mutational steps divergent.

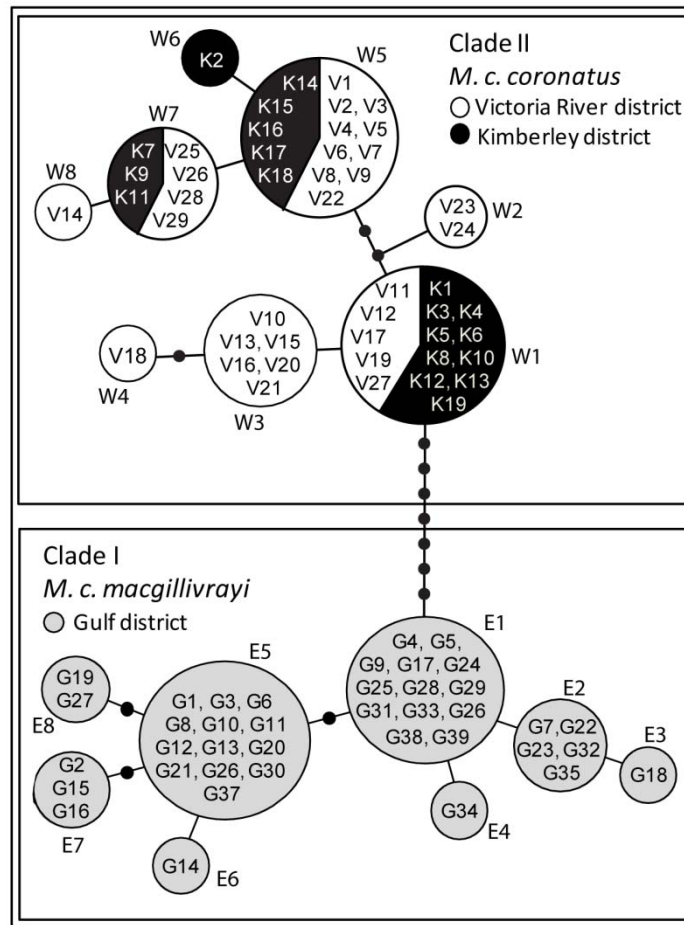


Figure 2.2. Unrooted haplotype network of *Malurus coronatus* ND2 sequences. The first letter in the sample codes represent the district from which the birds were sampled (G=Gulf; K = Kimberley; V = Victoria River) and are described in Table 2.1. Each haplotype is given a unique code: W1 to W8 are in the western subspecies (*M. c. coronatus*) and E1 to E8 are in the eastern subspecies (*M. c. macgillivrayi*).

The western clade ($N=48$, 8 haplotypes) was similarly structured, with two internal haplotypes that were both shared by 15 individuals and separated by three mutational steps (Figure 2.2). Three of the eight haplotypes in the western clade were shared between individuals from the western Kimberley and Victoria River. The haplotype most closely joined to the eastern polytomy was identified in 10 individuals from the Kimberley and five individuals from Victoria. The second large internal haplotype was conversely shared by 10 individuals from Victoria and five from the Kimberley. Of the remaining six haplotypes in the clade, one was shared (3 Kimberley, 4 Victoria), one was unique to the Kimberley, and four were unique to the Victoria River.

2.4.2. Phylogenetic analyses

ML, Bayesian analysis, and statistical parsimony all identified two groups that are consistent with an east/west subspecies division within *M. coronatus* (Figure 2.2 & 2.3). There was strong support for the hypothesis that the eastern and western subspecies formed separate clades on the tree, as all Bayesian trees in the posterior sample contained the western clade as monophyletic (Bayesian Posterior Probability of 1) with ML bootstrap support of 0.90 (Figure 2.3). Individuals from the western clade were separated by eight mutational steps from eastern sequences (Figure 2.2). There was little support for monophyly of the eastern clade due to variability in the rooting position of the out-groups. The root was positioned within the eastern clade in at least 50% of the trees and in the remainder of trees occurred between the two clades (Figure 2.3). There was no evidence of further phylogenetic divisions other than between *M. c. coronatus* and *M. c. macgillivrayi*.

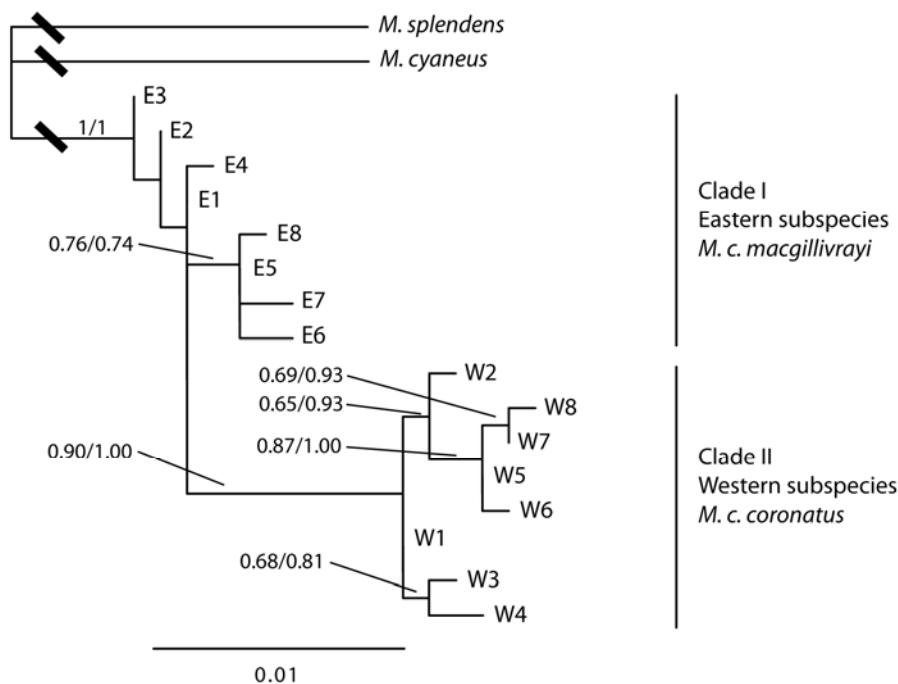


Figure 2.3. The Maximum Likelihood (ML) tree of *Malurus coronatus* ND2 haplotypes. For each node with bootstrap support >50% the ML bootstrap value is shown followed by Bayesian Posterior Probabilities. The sample codes represent the individual haplotypes (Figure 2.2). Haplotypes beginning with an (E) are from the eastern subspecies (*M. c. macgillivrayi*), (W) are from the western subspecies (*M. c. coronatus*). To improve clarity of the figure, only two outgroups are presented and branches with a diagonal bar are truncated.

2.4.3. Population genetics

The results of AMOVA indicated that most haplotype variation occurs between the three districts rather than between individuals within the same district (Table 2.2). Divergence was detected between the Gulf (*M. c. macgillivrayi*) and each of the two districts containing *M. c. coronatus* (Kimberley and Victoria). However there was no variance detected between populations of *M. c. coronatus* in Kimberley and Victoria districts (Table 2.3) indicating they belong to an interconnected population.

Table 2.2. Partitioning of genetic variation within and among the Kimberley, Victoria and Gulf districts using AMOVA.

Source of Variation	df	SS	MS	Variance	% Var.	ϕ - Statistic	Probability
Among Populations	2	202.42	101.21	3.59	77%	0.772	0.001
Within Populations	84	89.31	1.06	1.06	23%		
Total	86	291.72		4.66	100%		

Table 2.3. Pair-wise ϕ PT differences between the Kimberley, Victoria and Gulf districts using AMOVA.

Probability values ($p < 0.001 = **$, $p < 0.05 = *$) are calculated using 999 random permutations of ϕ PT and shown above the diagonal. ϕ PT is the fraction of the total variance that is among populations.

	Kimberley	Victoria	Gulf
Kimberley	-	0.321	0.001**
Victoria	0.000	-	0.001**
Gulf	0.827	0.813	-

2.4.4. Morphology

Adult *M. coronatus* were sexually dimorphic (Figure 2.4). Males were heavier than females (ANOVA $F_{1,343}=65.05$; $p<0.001$) and possessed longer bills (ANOVA $F_{1,350}=31.28$, $p<0.001$), larger head-bill length (ANOVA $F_{1,350}=171.34$, $p<0.001$), larger wings (ANOVA $F_{1,350}=247.22$, $p<0.001$), greater tarsus length (ANOVA $F_{1,350}=152.73$; $p<0.001$) and longer tails (ANOVA $F_{1,347}=45.38$, $p<0.001$).

The morphology of male (MANOVA $F_{12,268}=6.41$, $p<0.001$) and female (MANOVA $F_{12,242}=5.07$, $p<0.001$) purple-crowned fairy-wrens varied between the Kimberley, Victoria River and Gulf districts (Figure 2.4). Multicollinearity was not a problem for MANOVA as all morphological traits were correlated less than $r = 0.6$. A significant effect of latitude was identified on the common-slope of male head-bill length ($F_{1,186} = 6.52$; $p=0.011$), female tarsus ($F_{1,161} = 6.68$; $p=0.011$) and female wing length ($F_{1,161} = 6.62$; $p=0.011$), while the effect of latitude on male wing length differed within the three districts ($F_{1,184} = 4.25$; $p=0.041$). Confounding effects of latitude were controlled for in the results presented below.

Although eastern purple-crowned fairy-wrens weighed less (ANOVA females: $F_{2,127}=26.93$; $p<0.001$; males: $F_{2,143}=6.37$; $p=0.002$) and tended to be smaller than the western subspecies (Figure 2.4), we discovered incremental changes in body proportions between the three districts rather than a consistent scaling in body size between the subspecies (Figure 2.4). Males of the eastern subspecies had smaller bills (ANOVA $F_{2,149}=9.02$, $p<0.001$), shorter wings (ANCOVA $F_{2,149}=18.92$, $p<0.001$) and longer tails (ANOVA $F_{2,146}=12.83$, $p<0.001$) than their western counterparts. However, male head-bill size differed between the three districts (GLM $F_{2,148}=6.02$, $p=0.003$): males in the Gulf were comparably smaller than those in the Victoria River district ($t_{148}=2.16$, $p=0.032$), yet, not significantly different from those in the Kimberley ($t_{148}=0.66$, $p=0.512$). There was no overall difference in male tarsus length among districts (ANOVA $F_{2,149}=2.73$; $p=0.069$). Nevertheless, males in the Gulf had longer tarsi than those in the Kimberley (Contrast: $F_{1,187}=5.08$; $p=0.026$), even though there was no discernible difference between males in the Gulf and Victoria (Contrast: $F_{1,187}=3.07$, $p=0.082$). Females of the eastern

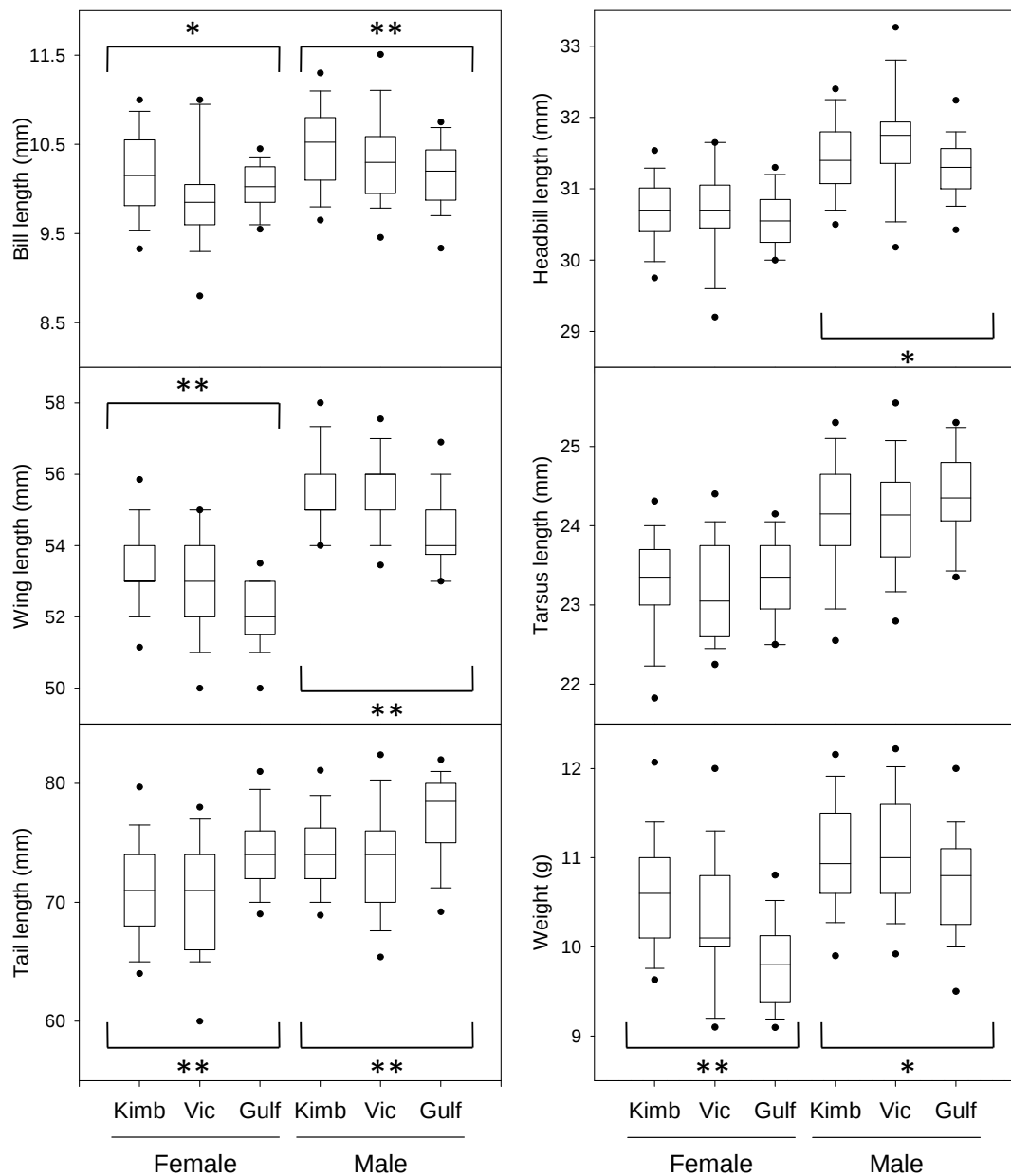


Figure 2.4. Morphological variation of male and female purple-crowned fairy-wrens sampled from the Kimberley (Kimb), Victoria (Vic) and Gulf districts. Asterisks indicate a significant difference in the variation of a morphological trait for given sex between districts: $p < 0.05 = *$; $p < 0.001 = **$.

subspecies had shorter wings (GLM $F_{2,127}=16.49$, $p<0.001$) and longer tails (ANOVA $F_{2,128}=9.49$, $p<0.001$) than those of the western subspecies. Bill length decreased incrementally from west to east (ANOVA $F_{2,128}=3.48$, $p=0.034$), with females in the Kimberley having larger bills than those in the Victoria River (Contrast, $F_{1,128}=5.67$, $p=0.019$). There was no discernible difference in female head-bill size (ANOVA $F_{2,128}=0.77$, $p=0.465$) or tarsus length (GLM $F_{2,127}=2.62$; $p=0.077$) between the districts.

2.5. Discussion

This study investigated the broad-scale population structure of *M. coronatus* to aid in determining management priorities and strategies for effective conservation. We identified two phylogenetic clusters across the range of *M. coronatus* (Figure 2.2 & 2.3), which corresponded with the two recognised subspecies (Schodde 1982). The genetic divergence between these subspecies is consistent with isolation by a natural barrier to gene-flow, and supports their separate management (DEWHA 2009; Garnett *et al.* 2011). The lack of genetic structure for ND2 within each of the two subspecies suggests that females were historically dispersing between the waterways in both the eastern and western section of the species range. The extirpation of purple-crowned fairy-wrens from the Ord River system (Skroblin and Legge 2010), is likely to disrupt dynamics in the remnant Victoria River and western Kimberley populations of *M. c. coronatus*, which although slightly morphological divergent (Figure 2.4), were highly connected by gene-flow over recent evolutionary time (Table 2.3).

2.5.1. Genetic divisions within M. coronatus

Our phylogenetic analyses revealed two clusters of ND2 sequences within *M. coronatus* that correspond with the phenotypically defined eastern *M. c. coronatus* and western *M. c. macgillivrayi* (Figure 2.2 & 2.3). The western subspecies forms a separate branch within the eastern subspecies, suggesting that *M. coronatus* may have originally occurred within the eastern portion of its range before colonizing the west. The lack of mitochondrial haplotype

sharing between the two subspecies indicates that there has been little or no successful migration of females between the two districts. Populations of *M. c. coronatus* on the Victoria River are separated by approximately 300km from populations of *M. c. macgillivrayi* in the Gulf (Figure 1.4). This barrier is comprised of semi-arid uplands that lack permanent water (Ford 1978), and thus the dense river-fringing vegetation *M. coronatus* requires (Rowley 1993; van Doorn 2007; Skroblin and Legge 2011). The northern portion of this barrier contains the headwaters of the Daly River catchment. Although *M. coronatus* has never been recorded within the Daly River catchment (Rowley 1993; Barrett *et al.* 2003), these waterways provide a likely route for previous connectivity between the subspecies. The Daly River drainage has been identified as a biogeographic barrier for other species in the monsoonal tropics (summarized in Eldridge *et al.* 2012). However, there was no evidence that the Ord arid intrusion, another major barrier in northern Australia (Bowman *et al.* 2010), influenced gene-flow between the western Kimberley and Victoria River (Figure 2.2 & 2.3).

The confirmation of a natural barrier to dispersal between the eastern and western populations of *M. coronatus* verifies the delineation of conservation management between the two subspecies (Rowley 1993; Garnett *et al.* 2011). As this study utilized a neutral marker, the signal of genetic divergence between the subspecies does not reveal evolutionarily relevant differences among populations (Halliburton 2004; Zink 2005). Likewise, the morphological change from east to west and decoupling of morphological body proportions (Figure 2.4), although possibly an adaptive response to local habitat structure or environmental conditions, may be a consequence of genetic drift. As a precaution however, we advocate that prospective management actions, such as translocations and captive-breeding programs, should maintain division between the eastern and western subspecies to preserve the integrity of potential adaptive divergence (Crandall *et al.* 2000; Moritz 2002).

2.5.2. Connectivity within subspecies

Although dispersal is prevented between *M. c. coronatus* and *M. c. macgillivrayi*, the lack of genetic structure for ND2 within each of these subspecies (Figure 2.2 & 2.3), suggests that females of both subspecies have been undertaking long-distance dispersal between the waterways that were sampled. The connectivity within *M. c. coronatus* was such that Victoria River and western Kimberley, which are now isolated by more than 200km, show no divergence in the frequency of haplotypes (Table 2.3). This finding is unexpected, as it is incongruent with behavioural observations which suggest this small passerine has limited dispersal capabilities (Rowley and Russell 1993) and the subsequent prediction that separate catchments contain isolated populations (Rowley 1993). A discrepancy between behavioural and genetic inferences of dispersal is not uncommon (for instance Fedy *et. al.* 2008; Howeth *et. al.* 2008), and occasional dispersal between catchments would be sufficient to prevent genetic divergence of neutral markers (Mills and Allendorf 1996). The slight morphological variation between fairy-wrens in the Kimberley and Victoria districts (Figure 2.4) suggests that, rather than belonging to a panmictic population, these districts contain separate subpopulations of *M. c. coronatus* that are linked by gene flow. Patterns of gene flow within the subspecies could be better investigated using more variable genetic markers, for instance microsatellites (Selkoe and Toonen 2006; Diniz-Filho *et. al.* 2008).

It is likely that natural patterns of dispersal within *M. c. coronatus* and *M. c. macgillivrayi* have been disrupted by the widespread degradation of riparian habitat that has occurred since pastoralism began in northern Australia around the turn of the 20th century (Rowley 1993; National Land and Resources Audit 2002). Degradation and fragmentation of habitat may isolate populations and place them at heightened risk of extinction from interacting genetic, demographic and environmental effects (Pimm *et. al.* 1988; Holsinger 2000; Ray 2001; Spielman *et al.* 2004), and furthermore prevent recolonization following extinction events (Fahrig and Merriam 1994). As female purple-crowned fairy-wrens undertake long-distance and between-river dispersal, decreasing connectivity between patches of habitat and associated

increases in hostile matrix may furthermore worsen the mortality of dispersing individuals (Brooker and Brooker 2001).

Of particular concern is the impact that contraction of *M. c. coronatus* (Smith and Johnstone 1977; Rowley 1993; Skroblin and Legge 2010) will have on connectivity between remnant populations of this Endangered subspecies. The extirpation of purple-crowned fairy-wrens from the Ord River system (Skroblin and Legge 2010), is likely to severely disrupt population dynamics within *M. c. coronatus*. Prior to anthropogenic degradation, populations across the range of *M. c. coronatus* were well connected by inter-catchment dispersal. Following the decline on the Ord River, the Victoria River population of *M. c. coronatus* is now isolated by a similar geographic distance from extant populations of *M. c. coronatus* in the western Kimberly as from populations of *M. c. macgillivrayi* in the Gulf. Although the Victoria population is genetically indistinguishable (Table 2.3) and only slightly morphologically divergent (Figure 2.4) from *M. c. coronatus* in the western Kimberley, it is likely that it will diverge from the other remnant populations of *M. c. coronatus* if connectivity is not restored.

2.5.3. Management directives

The priority for conservation management of *M. coronatus* must be the preservation of quality habitat and decreasing the risk of further population declines. As *M. c. coronatus* and *M. c. macgillivrayi* are isolated by a natural barrier to dispersal, management of these subspecies should be undertaken independently and the division between the subspecies maintained during interventions such as translocations and captive-breeding. Active conservation is more urgent for the Endangered *M. c. coronatus*, while the status of the eastern subspecies requires monitoring. It is likely that dispersal between waterways occupied by *M. c. coronatus*, and thus population dynamics, have been disrupted by wide-scale habitat degradation. As over-grazing is the major threat for purple-crowned fairy-wren habitat (Rowley 1993; van Doorn 2007; Skroblin and Legge 2011), it is important that management actions to reduce grazing pressure within riparian vegetation are implemented, especially where quality habitat occurs. Therefore,

conservation management of the *M. c. coronatus* could be further improved by information on the current extent, quality and arrangement of remaining habitat (Prugh *et al.* 2008), and the influence that habitat arrangement has on contemporary dispersal patterns (Fahrig and Merriam 1985; Holsinger 2000; Cox and Engstrom 2001). Conservation efforts will be best prioritized once the size and isolation of populations, and hence localized extinction risk (Pimm *et al.* 1988; Berger 1990), is known. Restoring connectivity between populations that are identified as having been isolated by habitat degradation is an important future conservation action.

CHAPTER 3

The distribution and status of the western subspecies of the purple-crowned fairy-wren (*Malurus coronatus coronatus*)

Citation: Skroblin, A., and S. Legge. 2010. The distribution and status of the western subspecies of the Purple-crowned Fairy-wren (Malurus coronatus coronatus). Emu 110:339-347.



Group of purple-crowned fairy-wrens in *Pandanus aquaticus*

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3.1. Abstract

Knowledge of the distribution of a species, although fundamental for directing conservation, is often lacking for rare or declining species or those occurring in remote locations. The western subspecies of the Purple-crowned Fairy-wren (*Malurus coronatus coronatus*) is a riparian habitat specialist of the Kimberley and Victoria River regions of northern Australia. Although listed as vulnerable nationally, there is little information on its current distribution and population trends. We conducted a comprehensive survey across 14 river catchments within the potential distribution of the subspecies, and identified changes in distribution by comparing the results of the survey with historical records. Western Purple-crowned Fairy-wrens were recorded on the Fitzroy, Isdell, Durack, Pentecost, Drysdale and Victoria River systems. The species was not detected in the Ord or the Sale systems despite previous reports, nor was it found in the Carson, Calder, Meda, Forrest, Berkeley or King George catchments. We suggest these last three catchments were wrongly included in previous estimates of the distribution of the species, when in fact Purple-crowned Fairy-wrens were potentially never there. We furthermore identify the populations of Purple-crowned Fairy-wrens most in need of conservation intervention and recommend excluding cattle to prevent further habitat degradation and population declines. These results are a crucial baseline from which to monitor future population trends of the Purple-crowned Fairy-wren and direct conservation management.

3.2. Introduction

Knowledge of the distribution of species and how this distribution is changing is fundamental for directing conservation management (Gibson *et. al.* 2004; Grenyer *et. al.* 2006). To direct conservation at the level of subpopulations, knowledge of distribution at a fine scale is furthermore required (Araújo and Williams 2000; Bottrill *et. al.* 2008; McDonald-Madden *et al.* 2008). For species that are rare, declining or located in inaccessible regions, detailed distributional information for conservation of subpopulations is often lacking (Boone and Krohn 2000).

The Purple-crowned Fairy-wren (*Malurus coronatus*; PCFW) is an example of a species whose past and current distribution, and population trends, are poorly known. The PCFW occurs across northern Australia, in the Kimberley region of Western Australia, the Victoria River region in the Northern Territory, and the south-western coast of the Gulf of Carpentaria of the Northern Territory and Queensland (Garnett and Crowley 2000; Higgins *et al.* 2001; Barrett *et al.* 2003). Although its overall distribution is expansive, the occurrence of the PCFW is highly localised. It is a riparian specialist, and restricted to the small patches of lush vegetation scattered along the rivers that dissect the vast tropical savannas of northern Australia (Rowley 1993).

PCFW are separated into two subspecies based on morphological differences: a western subspecies *M. c. coronatus* found in the Kimberley and Victoria River regions, and an eastern subspecies *M. c. macgillivrayi* found along the rivers that drain into the south-western Gulf of Carpentaria (Schodde 1982). The western species is listed as vulnerable nationally (*Environment Protection & Biodiversity Conservation Act 1999* (Aust.)) on the basis of declines in both population density and distribution (DEWHA 2009), though historical records are patchy (Rowley 1993). Specifically, three substantial declines are recorded. PCFW disappeared from the lower Fitzroy River with the introduction of sheep and cattle grazing (which removed habitat for PCFW) in the early 20th century. They disappeared from a large section of the Ord River following construction of the Ord River Dam and subsequent flooding of the area (Smith and Johnstone 1977; Rowley 1993). Finally, a more recent study in the Victoria River region reported ongoing population decline in response to intensive cattle grazing of river frontages (van Doorn 2007).

Western PCFW are currently believed to occur on the Victoria River in the Northern Territory and 11 river catchments in the Kimberley (Schodde 1982; Rowley 1993; Rowley and Russell 1993; Garnett and Crowley 2000; Johnstone and Storr 2004). However, this suggested distribution is based on records of varying credibility. Their occurrence in seven catchments – the Fitzroy, Isdell, Durack, Pentecost, Victoria, Drysdale and Ord – is corroborated by

numerous historical sightings (Figure 3.1), whereas their presence in the Sale–Berkelman catchment is suggested by just one unconfirmed sighting (Rowley 1993). Their occurrence on the Forrest, Berkley and King George rivers has been inferred by the presence of potentially suitable habitat (Rowley 1993) but their presence has never been confirmed. An accurate assessment of the current distribution of the species within the Kimberley and assessment of population trends is essential to the conservation of the western PCFW (TSSC 2008).

PCFW face continued pressure from land-management practices that threaten the integrity and quality of their habitat (Rowley 1993). In particular, introduced herbivores (cattle, Horses (*Equus caballus*) and Donkeys (*E. asinus*)) (Martin and McIntyre 2007), introduced weeds and an increase in the frequency of intense fires (Woinarski 1990; Rowley 1998; van Doorn 2007) have the potential to modify both the extent and the structure of riparian vegetation. The particular spatial arrangement of the PCFW – as small populations in patchily distributed habitat – makes the species potentially vulnerable to decline from loss of fairly small areas of habitat (Holsinger 2000). The sensitivity of PCFW to habitat degradation may be exacerbated by the complex social biology of the species: PCFW are sedentary cooperative breeders with limited dispersal abilities (Rowley 1993; van Doorn 2007).

We conducted extensive field surveys and use the results to document the current distribution of the threatened western subspecies of PCFW. We describe the most comprehensive and broad-scale investigation of the distribution of the PCFW in the Kimberley Region, which we believe to be the most comprehensive survey of any species in the region to date. We compare our results with the previous inferred distribution and the historical distribution, and discuss implications for conservation management, including the likely future population trends.

3.3. Methods

3.3.1. Study area

The study was conducted in the Kimberley region of northern Western Australia, and the Victoria River catchment in the Northern Territory. Together, these regions of the Wet–Dry Tropics encompass almost 550 000 km² of land and contain the entire distribution of the vulnerable western subspecies of the PCFW (Rowley 1993; Rowley and Russell 1997; Barrett *et al.* 2003). The land tenure is mixed, with almost 60% of the area being Pastoral leasehold land (this includes indigenous managed pastoral land), with the rest Unallocated Crown Land, Indigenous Reserve and Conservation Estate (Agriculture Western Australia 2001).

3.3.2. Study species

The cooperatively breeding PCFW is a small (10 – 13 g) riparian specialist of northern Australia (Schodde 1982; Rowley and Russell 1997). Groups of PCFW maintain territories, which are often arranged linearly along creeks and rivers, year round (Rowley and Russell 1993; Hall and Peters 2008). Its preferred habitat comprises a dense canopy of emergent *Eucalyptus* and *Melaleuca* trees and a well developed mid-storey of two distinct types. On most rivers in the Kimberley region, and some draining to the Gulf of Carpentaria, PCFW occur in areas where the midstorey is dominated by *Pandanus aquaticus* (Boekel 1979), which may be accompanied by a variety of shrubs, including Freshwater Mangrove (*Barringtonia acutangula*). In the Victoria River region and on lower sections of the Fitzroy River (Rowley 1993), PCFW are usually associated with areas of dense river grass dominated by *Chionachne cyanthopoda* (Rowley 1993; van Doorn 2007).

3.3.3. Collation of sightings

We collated historical reports of western PCFW from 1990, as records before 1993 were described by Rowley (1993). Historical data were gathered from published literature, the Atlas of Australian Birds (September 1998 – July 2007; Birds Australia, Melbourne), and from community members and birdwatchers in the Kimberley and Victoria River region (Figure 3.1).

We gathered 92 reports of PCFW from the Kimberley region and 49 from the Victoria River region made between the years 1990 to 2006 (Figure 3.1). For these years, there were records for the Fitzroy, Isdell, Pentecost, Drysdale, Durack, Ord, Sale–Berkelman and Victoria River systems. There were far fewer sightings reported before the start of the second Atlas of Australian of Birds, in 1998 (Barrett *et al.* 2003), with only 31 sightings between 1855 and 1993 (Rowley 1993).

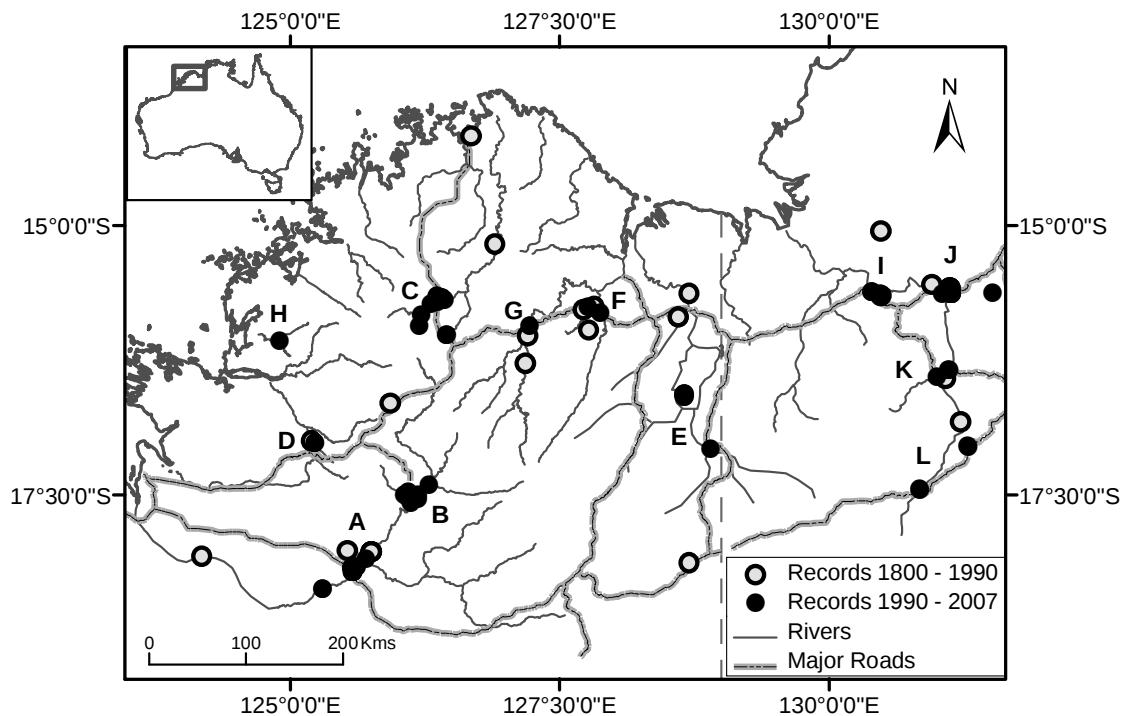


Figure. 3.1. Historical sightings of the western subspecies of Purple-crowned Fairy-wren across the range of the species. Sightings after 1990 are labelled: (a–h) Kimberley region: (a) Fitzroy River Crossing (n = 16); (b) Mornington Wildlife Sanctuary (n = 27); (c) Drysdale River Crossing (n = 28); (d) Bell Creek Campground (n = 4); (e) Ord River (n = 10); (f) Pentecost River Crossing (n = 2); (g) Jack’s Waterhole–Durack River Crossing (n = 1); and (h) Sale and Berkelman (n = 1); (i–l) Victoria River region: (i) Big Horse Creek Campground (n = 7); (j) Victoria River Bridge (n = 35); (k) Victoria River Downs (n = 3); and (l) Wave Hill (n = 4).

3.3.4. Survey design

Survey effort was directed towards the Kimberley region because the status of PCFW on the Victoria River has been recently assessed (van Doorn 2007). We surveyed for PCFW across 14 river systems within the potential range of the species: Fitzroy, Isdell, Meda, Pentecost, Drysdale, Durack, Forrest, Berkeley, King George, Sale–Berkelman, Calder, Ord, Carson and Victoria River systems (Table 3.1, Figure 3.2). These catchments included the entire set for which records of PCFW exist (seven) or where their presence has been inferred (three), plus an additional four catchments that neighbour the previous sets. Surveys were undertaken during the dry season in 2007 (May–Oct), 2008 (May–Oct) and 2009 (July). Within the 14 catchments, we targeted 97 locations (Table 3.1): 30 where the species had been previously sighted (to confirm their persistence at those sites), and 67 where the species had not been previously reported (to fill gaps in our knowledge of the true distribution).

In particular, we identified and focussed on six areas where knowledge of the distribution of PCFW was most deficient or conservation problems had already been identified. These were: (1) the lower Fitzroy River, where declines of PCFW in the early 20th century have been described (Smith and Johnstone 1977; Rowley 1993); (2) the Chamberlain and Pentecost rivers, where large numbers of PCFW were reported in the early 20th century, but not since; (3) the Forrest, Berkeley and King George rivers, where population estimates of 500 birds for each river (Rowley 1993) have never been confirmed by observations of the species; (4) the Durack River catchment, where birds were last sighted in the 1980s; (5) the Ord River, where the location of most sightings was submerged by the creation of Lake Argyle after construction of the Ord River Dam, and the most recent sightings, up to 2003, from one small area; and (6) the Sale and Berkelman rivers, where there was one unconfirmed sighting in 1992 (Rowley 1993).

Survey effort was secondarily directed towards assessing the extent of populations on the above river-systems, as well as the status of the PCFW in neighbouring catchments. The number of sites within each catchment varied with the size of the catchment, the extent of potential habitat available for survey and the location of the six areas of particular survey

importance (as above). The surveyed rivers traverse a total of 39 properties; each property was assigned to one of four land tenure types: (1) Conservation Land (National and Conservation Parks, plus pastoral land managed for conservation by Australian Wildlife Conservancy); (2) Indigenous Land Reserves (excluding indigenous pastoral); (3) Unallocated Crown Land; and (4) Pastoral Lands, including indigenous pastoral leases.

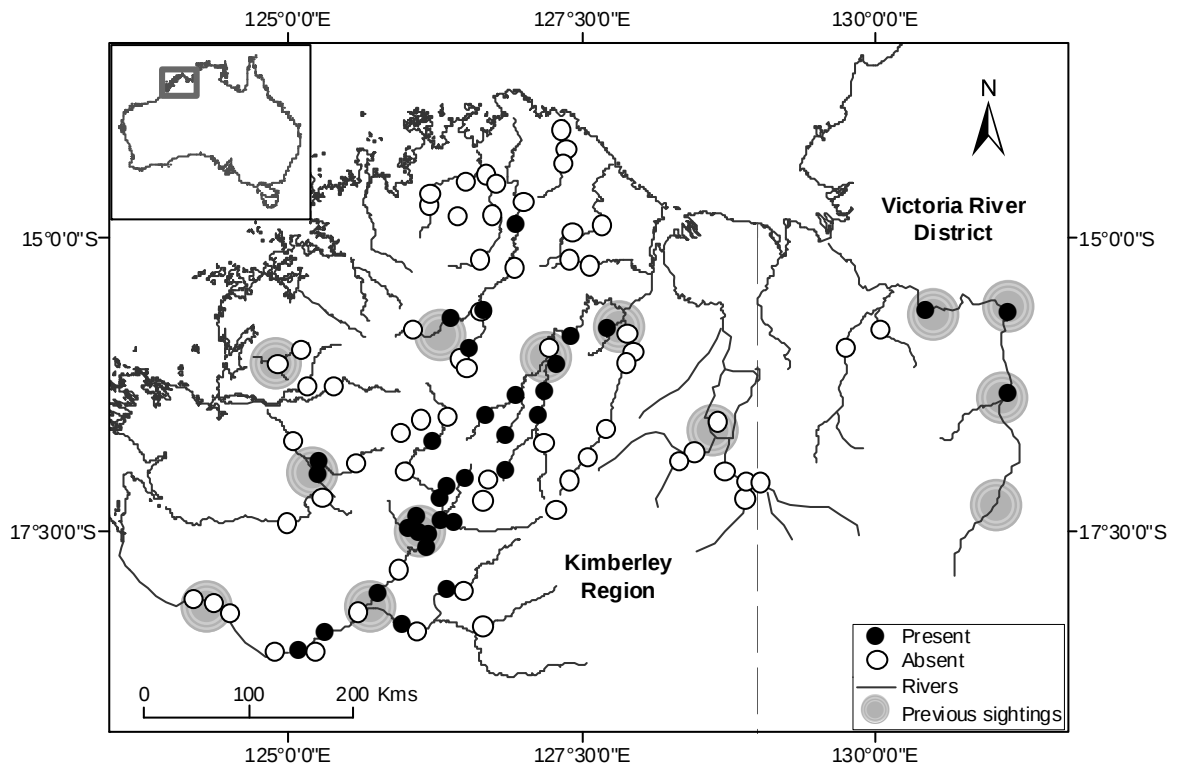


Figure 3.2. Locations surveyed for the western subspecies of Purple-crowned Fairy-wren during this study, 2007–09. Survey effort in the Kimberley region was directed to areas where knowledge of distribution was deficient or conservation problems had previously been identified. The locations of previous sightings are indicated. Sites are described in detail in the Accessory publication.

Table 3.1. Bird survey locations 2007 – 2009. Asterisks indicate expansions to previously described distribution of the Purple-crowned Fairy-wren. Locations prior to 1998 are from Rowley (1993).

River System	Site	Year	Name	Latitude	Longitude	Prior record	PCFW detected
Fitzroy	1	2007	Fitzroy River Liveringa	-18.07	124.18	1910	N
	2	2007	Fitzroy River Barrage	-18.10	124.35	~1925	N
	3	2007	Fitzroy River mid-lower	-18.19	124.49	~1925	N
	4	2009	Fitzroy River mid 2	-18.51	125.22	~1925	N
	5	2009	Fitzroy River mid 3	-18.51	125.08	-	Y*
	6	2009	Fitzroy River mid 4	-18.52	124.87	-	N
	7	2007	Cunningham River	-18.35	125.30	2007	Y
	8	2007	Fitzroy Crossing	-18.18	125.58	2001	N
	9	2007	Margaret River lower	-18.28	125.96	-	Y*
	10	2009	Margaret River mid	-18.33	126.08	-	N
	11	2009	Leopold & Little Gold Rivers	-17.99	126.49	-	N
	12	2009	Leopold River	-17.99	126.34	-	Y*
	13	2009	O'Donnell River lower	-18.30	126.65	-	N
	14	2007	Fitzroy River Geikie Gorge	-18.03	125.75	2007	Y
	15	2009	Fitzroy River Mid 5	-17.82	125.93	-	N
	16	2007	Spider Gorge	-17.63	126.17	-	Y*
	17	2007	Fitzroy River East	-17.43	126.39	2006	Y
	18	2008	Adcock River	-17.47	126.02	-	Y*
	19	2007	Annie Creek	-17.51	126.11	2007	Y
	20	2007	Roy Creek	-17.53	126.19	2007	Y
	21	2007	Yellow Creek	-17.11	126.34	-	Y
	22	2007	Hann Gibb River Road Crossing	-16.51	126.35	-	N
	23	2009	Hann Marion Downs	-16.73	126.23	-	Y*
	24	2007	Hann River Moll Gorge	-16.98	125.99	-	N
	25	2008	Hann River Glenroy	-17.21	126.26	-	Y*
	26	2007	Hann River Mornington	-17.39	126.29	2007	Y
	27	2008	Throssel River	-17.36	126.09	-	Y*
	28	2008	Clean Skin Pocket Creek	-17.05	126.70	-	N
	29	2008	Manning Creek	-16.65	125.95	1980	N
	30	2007	Traine River	-17.04	126.50	2007	Y
	31	2007	Idel Hole Creek	-17.23	126.65	-	N
	32	2007	Barnett River upper	-16.54	126.12	2004	N
Isdell	33	2007	Isdell Crossing	-16.91	125.57	-	N
	34	2008	Isdell River West Gorge	-16.73	125.03	-	N
	35	2008	Isdell River King Leopold CP	-16.90	125.25	-	Y*
	36	2007	Bell Creek	-17.01	125.23	2007	Y
Meda	37	2007	Lennard River King Leopold CP	-17.20	125.28	-	N
	38	2007	Lennard River Windjana Gorge	-17.42	124.98	-	N
Pentecost	39	2007	Pentecost Gibb River Road	-15.81	127.88	2001	N
	40	2007	Bindoola Creek	-15.78	127.77	2007	Y
	41	2007	Junction Pentecost and Chamberlain	-15.97	127.93	1901	N
	42	2007	Chamberlain near Pentecost	-16.06	127.87	-	N

Table 3.1. Cont.

River System	Site	Year	Name	Latitude	Longitude	Prior record	PCFW detected
Pentecost	43	2007	Chamberlain River mid 1	-16.62	127.69	-	N
	44	2007	Chamberlain River mid 2	-16.86	127.54	-	N
	45	2007	Chamberlain River Tributary	-17.31	127.27	-	N
	46	2007	Chamberlain River upper	-17.06	127.38	-	N
Drysedale	47	2007	Drysedale Crossing	-15.68	126.38	2007	Y
	48	2007	Plain Creek	-16.02	126.45	2005	N
	49	2007	Gibb River Kalumbaru Rd crossing	-16.10	126.51	-	N
	50	2009	Drysedale River Upper	-15.77	126.05	-	N
	51	2009	Gibb River Mid	-15.95	126.54	-	Y*
	52	2009	Drysedale River intersect Gibb River	-15.62	126.63	-	N
	53	2009	Drysedale River north of Gibb	-15.61	126.65	-	Y
	54	2009	Drysedale River north of Banjo Creek	-15.25	126.92	-	N
	55	2009	Drysedale NP 1	-14.89	126.94	-	Y
	56	2009	Johnston Creek	-14.69	126.99		N
Durack	57	2007	Durack Jack's Waterhole	-15.83	127.41	2007	Y
	58	2007	Durack Gibb River Rd crossing	-15.93	127.22	1999	N
	59	2007	Durack River Karunje Homestead	-16.30	127.18	2007	Y
	60	2007	Durack River mid	-16.51	127.13	-	Y*
	61	2007	Durack River upper	-16.74	127.17	-	N
	62	2008	Royston Creek	-16.08	127.28	-	Y*
	63	2007	Chapman River mid	-16.33	126.93	-	Y*
	64	2007	Chapman River upper	-16.51	126.67	-	Y*
	65	2008	Wood River Marion Downs	-16.97	126.85	-	Y*
	66	2007	Blackfellow Creek	-16.68	126.85	2007	Y
Forrest	67	2007	Forrest River mid	-15.23	127.56	-	N
	68	2007	Forrest River upper	-15.18	127.39	-	N
Berkeley	69	2007	Berkeley River mid	-14.89	127.66	-	N
	70	2007	Berkeley River upper 1	-14.95	127.41	-	N
King George	71	2007	King George River lower	-14.08	127.31	-	N
	72	2007	King George River mid	-14.24	127.36	-	N
	73	2007	King George River upper	-14.36	127.33	-	N
Sale	74	2008	Junction Sale and Berckelman	-16.07	124.90	1992	N
	75	2008	Sale upper	-15.94	125.10		N
Charnely	76	2008	Charnely River	-16.26	125.38	-	N
	77	2008	Calder	-16.25	125.15	-	N
Ord	78	2008	Ord River Everglades	-16.56	128.65	2002	N
	79	2008	Ord River lower	-16.98	128.71	-	N
	80	2008	Ord River mid	-17.21	128.88	-	N
	81	2008	Ord and Negri River junction	-17.07	128.90	1999	N
	82	2008	Negri River	-17.07	129.01	-	N
	83	2008	Bow River Lissadell	-16.82	128.45	-	N
	84	2008	Turkey Creek	-16.89	128.32		N

Table 3.1. Cont.

River System	Site	Year	Name	Latitude	Longitude	Prior record	PCFW detected
Carson	85	2009	Morgan Lower	-14.80	126.72	-	N
	86	2009	Morgan Upper	-14.81	126.43	-	N
	87	2009	King Edward Upper	-14.72	126.19	-	N
	88	2009	King Edward Mid	-14.62	126.20	-	N
	89	2009	King Edward Lower	-14.52	126.50	-	N
	90	2009	Carson Lower	-14.46	126.67	-	N
	91	2009	Carson Mid	-14.53	126.75	-	N
	92	2009	Carson Upper	-15.18	126.62	-	N
Victoria	93	2008	Victoria River - Big Horse Creek	-15.61	130.41	2007	Y
	94	2008	Victoria River Crossing	-15.63	131.13	2007	Y
	95	2008	Victoria River Dashwood Crossing	-16.33	131.11	2007	Y
	96	2008	East Baines	-15.77	130.05	-	N
	97	2008	West Baines	-15.92	129.74	-	N

3.3.4. Survey method

The 97 survey locations were accessed either by road (38 locations) or by helicopter (59 locations). Use of helicopter allowed us to remove the constraints of difficult ground access and moreover target patches of vegetation for survey that appeared to have the most suitable vegetation. To increase our chances of detecting PCFW on a river if they were present, we surveyed patches of vegetation that were long enough to contain territories (> 300 m) and that had a dense canopy of emergent trees, as well as a well-developed mid-storey (Wheeler 1965; Boekel 1979; Rowley 1993; van Doorn and Low Choy 2009). Either the entire patch (if < 1 km) or a minimum of 1 km of riparian vegetation was surveyed at each site.

To determine whether PCFW were present in a catchment, we aimed to survey a minimum of three patches of potential habitat, if available, on each section of river. We surveyed >300 km of river frontage in total. The longest survey distances were undertaken on large catchments where rivers were primarily accessed by road: the Fitzroy (200 km), Isdell, Drysdale (25 km each), Victoria (15 km) and Durack (10 km). The shortest survey distances were undertaken in catchments that were primarily accessed by helicopter and also happened to contain little habitat

to survey: Pentecost, Carson, Ord (5 km each), Forrest, Berkeley, King George, Sale and Calder (2 km each). Although survey distances were less in the last catchments, they included the habitat where PCFW were most likely to occur if present in the area. We have confidence therefore that findings in the surveyed areas are indicative of the status of the PCFW in each of the catchments.

Surveys for PCFW were conducted by walking sections of river, within or along the edge of riparian vegetation, listening for the distinctive calls of the species. The PCFW is highly territorial and extremely responsive to playback of territorial duets (Hall and Peters 2008; 2009), with 91% of dominant males and 87% of dominant females approaching within 10 m of playback speakers when just four territorial songs are broadcast (Hall and Peters 2008). We therefore used playback of PCFW territorial calls to increase our probability of detection during surveys. We broadcast a recording of PCFW calls at intervals of ~50 m within habitat patches. As territories may be 200 – 300 m long (Rowley and Russell 1993), our playback intervals were considered sufficient to encounter any resident birds. The 1.5-min recording consisting of six territorial duets played at ~10 s intervals was broadcast using anMP3 player (iRiver e10, Milwaukee, WI, USA) attached to hand-held speakers at a height of 1–2 m (Sony SRS-T57, Sony, Tokyo). In many instances individuals were detected by their soft, high-pitched contact calls (Higgins *et al.* 2001) or by unprompted territorial duets before playback was broadcast. In instances when PCFW were located before playback, the groups responded aggressively to subsequent broadcast of territorial duets.

Because group members other than the dominant pair often approach territorial threats (Hall and Peters 2008), the use of playback provided an additional aid in the estimation of the size of social groups. To improve the accuracy of the census, the 1.5 min playback recording was broadcast several more times once a group was detected, to encourage all group members to approach. As not all PCFW, including territorial individuals, may respond to playback (Hall and Peters 2008), two observers also listened for contact calls and scanned surrounding vegetation using binoculars to detect birds that may not have approached closely. A handheld GPS unit

(Garmin GPSmap 60, Schaffhausen, Switzerland) was used to record locations. To validate our survey method, we conducted a naïve survey within a monitored PCFW population where territorial boundaries were known and groups are regularly censused (Hall and Peters 2008; 2009). Along the 8 km of river surveyed, we were successful in detecting all monitored PCFW groups ($n = 21$). This suggests our method provides a high, although not perfect, probability of detection.

3.3.5. Social composition of groups

The social composition of each territorial group encountered during survey work was recorded. Birds were identified as the breeding individuals if they performed territorial duets (Rowley and Russell 1993; Hall and Peters 2008; 2009), or solo versions of the territorial song in response to playback. All group members other than the territorial pair were classified as subordinates. As groups are highly cohesive (Rowley and Russell 1993), we classified birds as solo when they responded to playback alone and no other PCFW were detected within 200 m.

3.4. Results

3.4.1. Survey findings

In total, 197 territorial groups were discovered at 34 of the 97 survey locations (Figure 3.2; Table 3.1). Territories were defended by 1–8 individuals, with a mean group size ($\pm$ s.e.) of 3.1 ± 1.6 individuals. Groups most frequently comprised a breeding pair with no subordinates (40.6%); one subordinate was present in 19.8% of groups (Table 3.2).

There had been confirmed records of PCFW on seven catchments (Figure 3.1). We detected PCFW on six of these (Fitzroy, Isdell, Durack, Pentecost, Drysdale and Victoria rivers) (Figure 3.3). We failed to detect PCFW in the Ord River catchment. PCFW were not detected on the remaining six surveyed catchments, including the Meda (2 sites), Carson (8 sites), Berkeley (2 sites), King George (3 sites), Forrest (2 sites), or Sale–Berkelmen (2 sites) (Figure 3.2). We did not survey the 14th catchment (Victoria) extensively because detailed studies have been carried

out there recently (van Doorn 2007). The species was detected on 16 of the 39 properties surveyed. Of these, eleven were pastoral lands, four were conservation lands and one was vacant crown land (Figure 3.4).

Table 3.2. Summary of the survey for *M. c. coronatus* and the social composition of encountered territorial groups

The species had been previously reported in the Ord and Sale river systems, but they were not located during the 2007–09 surveys. Sites on the Forrest, Berkeley, King George, Sale, Calder, Ord and Carson River catchments were accessed by helicopter and the habitat surveyed is the most suitable on those catchments. Birds were classified as *breeding* if they performed territorial duets, *solo* if responding to playback alone with no other PCFW detected within 200 m, and *subordinate* if a group member other than the territorial pair.

Catchment	# Sites	Present (% sites)	Territories	Breeding birds	Sub- ordinates	Solo birds	Total
Fitzroy	32	50	96	182	123	5	310
Isdell	4	50	11	18	9	2	29
Meda	2	0	0	0	0	0	0
Pentecost	8	12	4	8	9	0	17
Drysdale	10	40	24	38	21	5	64
Durack	10	80	32	54	22	5	81
Forrest	2	0	0	0	0	0	0
Berkeley	2	0	0	0	0	0	0
King George	3	0	0	0	0	0	0
Sale	3	0	0	0	0	0	0
Calder	1	0	0	0	0	0	0
Ord	7	0	0	0	0	0	0
Carson	8	0	0	0	0	0	0
Victoria	5	60	30	58	39	1	98
Total	97	35	197	358	223	18	599

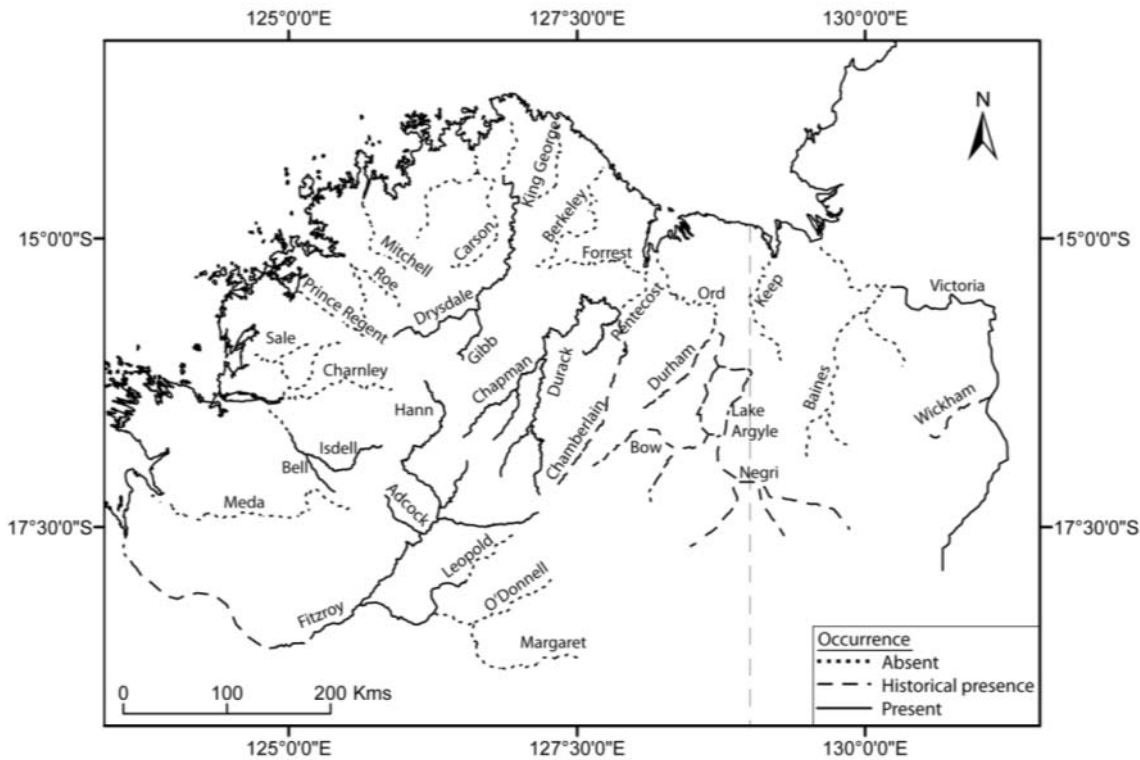


Figure 3.3. The distribution of the western subspecies of Purple-crowned Fairy-wren (PCFW) in 2010. The solid lines represent sections of rivers where PCFW have been sighted since 2007. The dashed lines represent sections of river where PCFW were sighted before 2007 but could not be located by the current survey. The dotted lines represent rivers where PCFW have never been found (based on Rowley 1993).

In the following section we describe the results of our survey from six areas of particular survey importance (as outlined in Methods 3.3.4.):

Fitzroy River catchment

We confirmed the presence of a population of PCFW at low density near the Fitzroy Crossing township (Rowley 1993), with groups located in Geike Gorge National Park (site 14) and on the Cunningham River on Jubilee Downs Station to the south (site 7) (Figure 3.4). Despite finding small patches of river grass habitat (*Chionachne cyathopoda*), we were unable to detect PCFW along the lower Fitzroy on Liveringa Station where the species was last

reported in the early 20th century (sites 1, 2 and 3). The group furthest downstream within the Fitzroy River catchment was in an isolated patch of river grass ~30 km downstream (site 5; Figure 3.2) of the previously estimated boundary of the population at Jubilee Downs Station (Rowley 1993) (site 7).

Within the Fitzroy River catchment, we located PCFW for the first time on the lower Margaret River (6 groups), the Leopold River (1 group), Spider Creek (3 groups), the Throssell River (22 groups), the Traine River (13 groups) and the Hann River (31 groups). Although habitat appeared suitable, we were unable to confirm the presence of PCFW on Manning Creek (Smith and Johnstone 1977; Rowley 1993). Large and dense populations of PCFW were found north of Dimond Gorge in the middle to upper reaches of the Hann and Adcock rivers and their tributaries.

Chamberlain and Pentecost River catchments

We confirmed the presence of PCFW at the intersection of the Gibb River Road with Bindoola Creek, a tributary of the Pentecost River (1 group, site 40; Figure 3.2). A further three territorial groups were found several kilometres further west (Table 3.2). We were unable to detect PCFW at four sites along the Chamberlain River. No habitat was located near the Pentecost and Chamberlain River junction, or at the Gibb River Road crossing of the Pentecost River where sightings of the species were previously reported (Barrett *et al.* 2003). The species therefore appears to be limited to Bindoola Creek within this catchment.

Forrest, Berkeley, King George rivers

Owing to the remoteness of these rivers, survey sites were accessed by helicopter. Although vegetation with high habitat potential was surveyed with playback, no PCFW were detected on the Forrest (2 sites), Berkeley (2 sites) or King George (3 sites) rivers. Riparian habitat was sparsely distributed along these rivers. Occurrence of PCFW at other sites within these catchments was unlikely as there were only three additional patches of potential habitat

available on the Forrest and Berkeley rivers and another 10 potential patches on the King George River.

Durack River catchment

This survey confirmed for the first time the presence of PCFW on the middle reaches of the Durack River. PCFW were located in large and dense patches of habitat on Karunje Station (3 sites, 18 groups), the Chapman River (2 sites, 11 groups), Blackfellow Creek (1 site, 1 group) and Wood River (1 site, 2 groups) (Figure 3.2). In total, 81 groups were located within the ~10 km of river surveyed (Table 3.1). Although the population appears extensive, only two previous sightings (Rowley 1993), both from the 1980s (at Karunje homestead and Jack's Waterhole), could be found for the catchment.

Ord River catchment

We were unable to locate PCFWs at the Ord River Everglades, where the species had been sighted intermittently until 2003 (site 5; Figure 3.2) or at a further six sites upstream from Lake Argyle. Owing to prolonged inundation after a rise in water levels in Lake Argyle, vegetation structure had been modified at the Ord River Everglades (Katrina Nissen, Environmental Officer, Argyle Diamond Mine, Kununurra, pers. comm.). At the time of our visit (August 2008) riparian verges in the area supported some large trees and a ground cover of low-growing weeds. An understorey of shrubs, *Pandanus* or river grasses, essential to the PCFW for shelter, foraging and nesting (Wheeler 1964; Boekel 1979; Rowley 1993; van Doorn and Low Choy 2009) was completely absent. Habitat was highly degraded with large numbers of livestock, widespread weed invasion and erosion of river banks evident.

Sale River catchment

We were unable to confirm a sighting of PCFW reported for the junction of the Sale and Berkelman rivers on Pantijan Station (Rowley 1993). Habitat at the junction (site 74) was of marginal quality. The species was not detected there or in apparently more suitable habitat at other locations within the catchment (site 75) and on the neighbouring Calder River (Figure

3.3). The traditional owner of Pantijan, Lennie Jorda, could not recall having seen PCFW on the property.

Other important results include confirming the continued existence of a dense population of PCFW at Drysdale River Crossing (site 47) and a small population downstream in Drysdale National Park (Rowley 1993). We also confirmed the presence of a small population of PCFW on the Isdell River within the King Leopold Conservation Park: there were nine territorial groups along 5 km of the Bell Creek tributary of the Isdell (site 36; Figure 3.2), and two groups on the Isdell River on the north-eastern boundary of the conservation park (site 35; Figure 3.2).

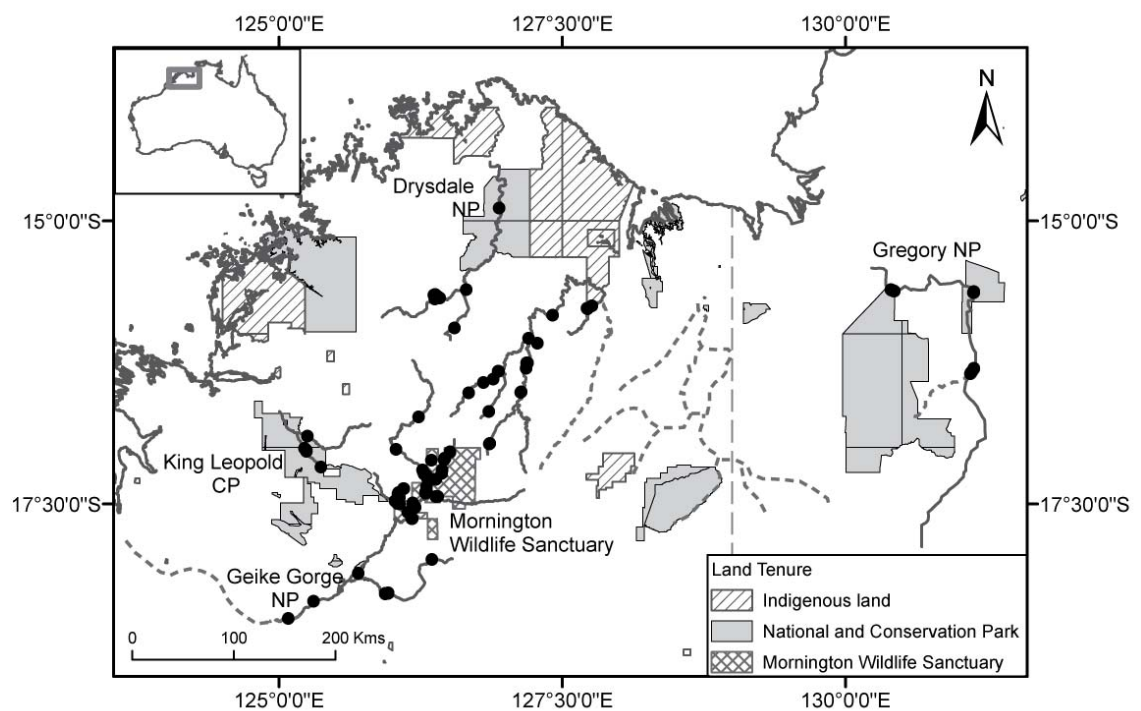


Figure 3.4. Location of territories of the western subspecies of Purple-crowned Fairy-wren (PCFW) found during 2007–09 with respect to land tenure. Dark lines are rivers where PCFW currently occur; dashed lines represent sections of river where PCFW were sighted before 2007 but not located during the current survey. Names of conservation land where PCFW were located are indicated. Pastoral properties and Crown Land are not shaded.

3.5. Discussion

The survey we conducted, coupled with the collation of recent confirmed observations, refine our understanding of the distribution and population trends of the western subspecies of the Purple-crowned Fairy-wren, and the conservation implications for the subspecies.

3.5.1. Current distribution

Our survey results suggest that the subspecies is now confined to six river systems: the Fitzroy, Isdell, Durack, Pentecost, Drysdale and Victoria (Figure 3.3). This contrasts with the previously published distribution of the species, which included another five catchments: the Forrest, Berkeley, King George, Sale–Berckelman and Ord River catchments (Rowley 1993; Garnett and Crowley 2000; Barrett *et al.* 2003; Johnstone and Storr 2004). We excluded these five catchments from the updated distribution because we were unable to locate PCFW during surveys of the most suitable habitat within these areas or find any other recent confirmed records of the species. Of these five catchments, however, historical occupancy, and therefore recent decline, could only be established for the Ord as there have been no confirmed sightings reported for the others.

We suggest that the PCFW was never present on the Forrest, Berkeley and King George rivers and suggest the sighting for Sale–Berckelman rivers may have been in error because there is no other evidence to support recent occupancy. The presence of PCFW on the Forrest, Berkeley and King George rivers was previously inferred from availability of *Pandanus* habitat, but in the absence of records or surveys (Rowley 1993). Although we confirmed the presence of *Pandanus* on the Forrest, Berkeley and King George rivers (Rowley 1993), its suitability as habitat may have been overestimated. *Pandanus* generally grew as small dense patches in the middle of the river, and was thus subject to high rates of flooding during the wet season, but lacked an overstorey that would provide refuge for PCFW during floods (Rowley and Russell 1993). Habitat that appeared suitable was limited in extent and sparsely distributed along these rivers, therefore the persistence of isolated, yet viable populations, of PCFW on these rivers is

further unlikely (Hanski 1998; Fahrig 2001; Theodorou and Couvet 2009). As the presence of species are often predicted by the location of habitat across landscapes (Guisan and Zimmermann 2000; Osborne *et. al.* 2001; Angelstam *et. al.* 2004), the absence of PCFW from these rivers demonstrates the importance of on-ground evaluation of distribution estimates.

The PCFW occurs only in the mid-sections of large river catchments which drain the Central Kimberley Plateau. It appears to be absent from the more coastal river systems, including the Forrest, Berkeley and King George rivers in the far north-east, the Sale–Berckelman rivers in the far west and four other catchments (Prince Regent, Roe, Mitchell and Carson). These rivers on the northern and north-western coastal rim of the Kimberley are recognised as some of the least-stressed rivers in northern Australia (National Land and Resources Audit 2002). However, they may be generally less suitable for PCFW if higher rainfall and rates of flooding make the available habitat unsuitable during the wet season (Kilgour 1904; Rowley 1993; van Doorn 2007). Moreover, barriers to dispersal may also prevent colonisation of these coastal catchments. PCFW are resident species with rather poor flight capabilities (Rowley 1993; Rowley and Russell 1993). It is therefore unlikely the species would disperse across the vast distances of inhospitable land from the central Kimberley populations to coastal catchments. For PCFW populations to occur along these isolated rivers they would need to be large to remain viable (Pimm *et al.* 1988; Holsinger 2000), and would therefore have likely been encountered during our surveys.

3.5.2. Population trends

Declines of the PCFW have been documented in the Kimberley (Smith and Johnstone 1977; Rowley 1993), and on the Victoria River (van Doorn 2007). The PCFW disappeared from the lower Fitzroy River in the early 20th century following the introduction of grazing in the Kimberley (Smith and Johnstone 1977; Rowley 1993). The continued absence of the species from this area indicates either permanent damage to habitat or a limited ability of the species to recolonise the area from elsewhere. The PCFW also disappeared from a large section of the Ord

River when habitat was submerged after construction of the Ord River Dam (Smith and Johnstone 1977; Rowley 1993). Although the species was repeatedly sighted until 2003 at the Ord River Everglades upstream from the Dam, we had no more recent sightings and did not detect PCFW in our surveys of the catchment. The disappearance of the PCFW from the Ord River catchment is likely to be the culmination of a population decline following construction of the dam in combination with ongoing loss and degradation of riverine vegetation through grazing, weed encroachment and intense fires (McKenzie *et. al.* 2009). As it was beyond the scope of this study to re-visit sites, we recommend future surveys of the Ord River to search for potential remnant populations.

Except for the disappearance of the PCFW from the lower Fitzroy and Ord rivers, overall population trends of PCFW in the Kimberley are poorly known. Although there were many sightings of the PCFW within seven catchments between 1990 and 2006, the sightings cluster around locations with easy road access (Figure 3.1). The highest number of sightings occurred at the popular tourist destinations of Fitzroy Crossing ($n = 16$), Mornington Wildlife Sanctuary ($n = 27$) and Drysdale Station ($n = 28$) in the Kimberley, and Victoria River Bridge Crossing ($n = 35$) in the Victoria River region. Most other sightings are associated with camping sites and public road crossings of rivers reflecting ease of access to riverine areas (Figure 3.1). It is difficult to detect population change from a baseline of historical sightings that are biased by accessibility and limited in distributional coverage.

Fine-scale historical information is available only for the Drysdale River Crossing population of PCFW studied by Rowley and Russell (1993). The pattern of PCFW territories uncovered by the current survey is quite similar to that described in the 1980s (Rowley and Russell 1993), suggesting that habitat has not since deteriorated to the extent that precipitates large-scale declines. Such fine-scale historical information is unfortunately lacking for all other populations of PCFW and population trends are therefore unknown. This survey provides a much more comprehensive knowledge of the distribution of the PCFW, and includes some range extensions. In particular, we found additional large populations of PCFW in the mid-

reaches of the Fitzroy and Durack catchments and small populations in the Isdell and Pentecost catchments. An assessment of the extent and location of habitat within each catchment would further refine knowledge of fine-scale distribution of PCFW.

The ongoing degradation and loss of riparian vegetation in northern Australia (National Land and Resources Audit 2002) places populations of PCFW at risk of continued decline. The majority of PCFWs in the Kimberley occur on pastoral land, with only a small proportion of the populations present within protected areas (Figure 3.4). The situation is similar in the Victoria River region, where only a small proportion of river frontage is on conservation land. Although declines have only been confirmed on the Fitzroy, Ord and Victoria rivers (van Doorn 2007), declines in other areas are likely because of the deterioration in the condition of riparian zones through grazing by livestock, changed fire regimes and introduction of weeds (McKenzie *et al.* 2009). Unless practices to limit degradation of riparian areas are implemented, we can expect further declines of the PCFW across the range of the species.

3.5.3. Conservation directions

The recent disappearance of PCFWs from the Ord River together with the historical decline from the lower Fitzroy and the ongoing decline on the Victoria River (van Doorn 2007) signal the need for a targeted approach to conservation management. In the absence of genetic data to identify specific management (Palsboll *et al.* 2007) or evolutionary significant units (Moritz 1994; Crandall *et al.* 2000), it is appropriate to consider each isolated catchment as containing a conservation management unit. Conservation measures for the PCFW can thereby be tailored to the individual threats faced by, and the needs of, each of these subpopulations.

The most urgent conservation effort may be required by the smallest subpopulations on the Isdell and Pentecost catchments. These small populations face a higher risk of extinction unless linked to other populations through dispersal (Pimm *et al.* 1988; Holsinger 2000). Protection of these populations could be improved by excluding herbivores from the small lengths of river frontages that contain the PCFWs. Elsewhere, broad-scale conservation measures are required

to maintain populations of PCFW. Management to limit grazing of riparian areas is an important conservation measure, but fencing of riparian areas to exclude stock (van Doorn 2007) is not feasible across vast distances, especially when fencing would be damaged by floods annually in each wet season. Provision of watering points away from riparian areas may be a better option to discourage stock from spending time at river frontages. Landscape-scale fire management is required to reduce the incidence of intense and extensive fires that are known to damage riparian vegetation. We also recommend initiation of a strategic monitoring program for timely detection of future declines, using the reliable baseline estimate of their current distribution that we report here. As well as monitoring for the continued presence of PCFW, we recommend carrying out habitat assessments to identify riparian degradation and provide the opportunity for restoration before declines in riparian species occur.

CHAPTER 4

The influence of fine-scale habitat requirements and riparian degradation on the distribution of the purple-crowned fairy-wren (*Malurus coronatus coronatus*) in northern Australia

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Pandanus dominated purple-crowned fairy-wren habitat

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4.1. Abstract

Species distributions are influenced by variation in environmental conditions across many scales. Knowledge of fine-scale habitat requirements is important for predicting species occurrence and identifying suitable habitat for target species. Here we investigate the perplexing distribution of a riparian habitat specialist, the western sub-species of the purple-crowned fairy-wren (*Malurus coronatus coronatus*), in relation to fine-scale habitat associations and patterns of riparian degradation. Surveys of vegetation attributes, river structure and disturbance indicators that are likely to be causal determinants of the species occurrence were undertaken at 635 sites across 14 catchments. Generalized Linear Mixed Modelling demonstrated that the probability of purple-crowned fairy-wren occurrence increased with *Pandanus aquaticus* crown cover, shrub density and height of emergent trees, while riparian structure and signs of cattle were indirect predictors of occurrence. As our study area predominantly contained *Pandanus* type habitat, we failed to identify river-grass as an important component of habitat. Predictions from a cross-validated model of purple-crowned fairy-wren occurrence suggested distribution is constrained by three factors: 1) low quality of local habitat within catchments where the species occurs, 2) broad-scale reduction in habitat quality that has resulted in extinction of the species from parts of its range, and 3) unmeasured variables that limit the exploitation of suitable habitat. The reliance of the species on dense shrubby understorey suggests conservation efforts should aim to maintain the complexity of understorey structure by managing fire and grazing intensity. Efforts to halt the continuing decline of riparian condition and maintain connectivity between areas of quality habitat will help to ensure persistence of riparian habitat specialists in northern Australia.

4.2. Introduction

Understanding the interactions between species distributions and the abiotic and biotic environment is vital for identifying areas of high-quality habitat and predicting species distributions (Angelstam *et al.* 2004; Rodriguez 2007). Species distributions can be influenced by environmental conditions across many scales; from the fine-scale conditions experienced by an individual, to the landscape-scale conditions that influence population structure and demographics (Wiens 1989; Boone and Krohn 2000; Turner 2005). The strength of the association between distribution and features of the environment differs depending on whether organisms are habitat specialists or generalists (Lavorel *et al.* 1997; Attum *et al.* 2006). Due to their narrow niche, habitat specialists may be more at risk from modification of habitat (natural or anthropogenic) than habitat generalists (Pimm *et al.* 1988; Henle *et al.* 2004; Devictor 2008). Thus, knowledge of habitat associations may be especially important for understanding the factors that influence the distribution and abundance of rare or declining habitat specialists.

Species that are endemic to riparian areas in northern Australia are experiencing an ongoing decline in the quality of their riparian habitat (National Land and Resources Audit 2002) as a consequence of altered fire regimes (Woinarski 1990; Russell-Smith *et al.* 2003; Valentine *et al.* 2007), weed incursion, and grazing by introduced herbivores (Rowley 1993; McKenzie *et al.* 2009). The ecological impacts of the decline in the quality of riparian habitat are broad; riparian areas in northern Australia are generally more productive than the surrounding savannah-woodland habitats (Russell-Smith 1991; Woinarski *et al.* 2000) and support a multitude of taxa, including an especially rich avifauna (Woinarski *et al.* 2000). Nevertheless, conservation management of this habitat has gained limited attention because there are relatively few endemic and threatened riparian specialists (Woinarski *et al.* 2000). Riparian habitat specialists however, could serve as important biological indicator species (Cairns *et al.* 1993) for the health of riparian habitat.

One of the endemic and threatened riparian specialists of northern Australia is the western sub-species of the purple-crowned fairy-wren *Malurus coronatus coronatus* (Higgins *et*

al. 2001; Barrett *et al.* 2003). As is the case for many rare or declining species (Araújo and Williams 2000), the distribution of the purple-crowned fairy-wren in relation to habitat parameters is poorly understood. Regional surveys have described preferences of *M. c. coronatus* for habitat dominated by the grass *Chionachne cyanthopoda* on the Victoria River (van Doorn 2007; van Doorn and Low Choy 2009). In the Kimberley region, the species appears to have disappeared from areas where *Chionachne cyanthopoda* was heavily grazed at the beginning of the 20th Century (Smith and Johnstone 1977; Rowley 1993), but persists in areas with *Pandanus aquaticus* (Rowley 1993; Rowley and Russell 1993). Although the species is associated with two distinct types of habitat, it only occurs on a subset of the drainages in the Kimberley and Victoria River regions that contain these vegetation types (Rowley 1993; Higgins *et al.* 2001; Barrett *et al.* 2003; Skroblin and Legge 2010); the reason for this patchy distribution is unknown.

To improve conservation management of this riparian habitat specialist, it is important to establish which factors, beyond the occurrence of *Pandanus* and river-grass, influence the distribution and abundance of the species. Declines in both habitat types have previously been attributed to degradation caused by grazing of introduced herbivores, weed incursion, and repeated intense fires (Smith and Johnstone 1977; Rowley and Russell 1993; Garnett and Crowley 2000; Skroblin and Legge 2010). However the response of the fairy-wren to disturbance factors has only been quantitatively attributed to grazing in the Victoria River (van Doorn 2007). Evidently, a regional-scale study of the species habitat associations and the impact of habitat degradation on its distribution is required.

We aim to understand the distribution of the purple-crowned fairy-wren in relation to fine-scale habitat parameters and riparian degradation. We measured environmental variables that are likely to be causal determinants of the species occurrence within the following three themes: 1) vegetation attributes, 2) riparian structure, and 3) disturbance indicators. We aimed to model the parameters that influence the distribution of the species and use this information to investigate the disappearance or absence of the species from catchments. Knowledge of how

fine-scale habitat associations influence the distribution of the purple-crowned fairy-wren will increase our understanding of how the on-going decline in riparian quality in northern Australia (National Land and Resources Audit 2002) could impact on this species and others that rely on riparian habitat. The extent to which species distributions are influenced by habitat quality can help direct conservation management to limit habitat degradation.

4.3. Methods

4.3.1. Survey design

The study was conducted in the Kimberley region of Western Australia and the Victoria River district in the Northern Territory during the dry seasons in 2007 (May-Oct), 2008 (May-Oct) and 2009 (July). Within the constraints of limited accessibility in this remote region (van Doorn 2007; Skroblin and Legge 2010), survey locations were chosen to maximise the diversity of riparian habitat sampled. Survey effort included all five catchments where the western purple-crowned fairy-wren currently occurs (Skroblin and Legge 2010). Access to rivers was gained at 33 locations (upper Fitzroy = 22, Durack = 2, Isdell = 4, Drysdale = 2, Victoria = 3), which were generally tens of kilometres apart within the same river-system. Survey effort also included areas from which *M. c. coronatus* has disappeared (lower Fitzroy = 4 and Ord = 2 access points), to investigate the current condition of habitat in these areas. Finally, neighbouring catchments where the species has never been recorded (Barrett *et al.* 2003; Skroblin and Legge 2010) were also surveyed to ascertain whether the lack of suitable habitat prohibits occurrence on these rivers (Forrest = 2, Berkeley = 2, King George = 3, Sale/Berkelman = 2, Calder = 2, Meda = 2 and Carson = 8 access points gained). Multiple sites were surveyed from most access points.

4.3.2. Survey method

Riparian habitat attributes were recorded in conjunction with surveys for the presence *M. c. coronatus* (Skroblin and Legge 2010). As the purple-crowned fairy-wren is associated with

dense riparian vegetation (Rowley and Russell 1993; van Doorn and Low Choy 2009), survey effort was directed to areas that contained at least some riparian vegetation structure. Surveys were conducted by walking along the river bank, within or next to riparian vegetation, using broadcasts of *M. c. coronatus* territorial calls to assist in detection of this highly territorial species (Hall and Peters 2008). We used a playback interval of 50 m as the species responds readily to playback from distances up to 50 m (Skroblin and Legge 2010), and it should be sufficient to detect territories which average 150 m in length (Kingma *et al.* 2009) in the mid-Fitzroy catchment and range between 200-300 m in the Drysdale catchment (Rowley and Russell 1993). Descriptors of riparian habitat (Table 4.1) were recorded within a ten metre radius of sites where playbacks were broadcast. At each survey site, the presence or absence of fairy-wrens was ascertained and riparian habitat was quantified.

4.3.3. Measurement of habitat attributes

To increase the likelihood of measuring causal predictors of purple-crowned fairy-wren presence (Guisan and Thuiller 2005), we used previous descriptions of the species habitat use and ecology (Boekel 1979; Rowley 1993; Woinarski *et al.* 2000; van Doorn 2007) when choosing riparian attributes to measure. Measurements were based on the methods of Dixon *et al.* (2006) and riparian attributes were grouped into the three themes:

Vegetation attributes

The purple-crowned fairy-wren is associated with *Pandanus aquaticus* and river grasses (such as *Chionachne* spp.), and uses these shrub-layer vegetation structures for nesting, foraging, and shelter (Officer 1964; Wheeler 1965; Rowley and Russell 1993; van Doorn 2007). The species has been observed using canopy to escape from flood waters (Rowley and Russell 1993; van Doorn and Low Choy 2009). Accordingly, we measured the area and crown cover of any *Pandanus aquaticus* stand, the cover and height of grasses, the cover of other shrubs and trees up to 4 m in height, plus canopy height and canopy cover within our 10 m survey radius (Table 4.1).

Table 4.1. Description of fine-scale habitat attributes recorded at sites surveyed for the presence of the purple-crowned fairy-wren (N= 635).

Variable	Mean	S.E.	Description
Occurrence (0/1)			Absent /present by playback survey
<i>Vegetation</i>			
Canopy height (m)	12.67	0.23	Maximum height of trees
Canopy cover (index)	2.32	0.05	Percentage canopy cover (<5, 5-50, >50%)
Shrub density (index)	1.68	0.07	Cover of shrubs and small trees 1.5 – 4m (<5, 5-50, >50%)
<i>Pandanus</i> cover (index)	1.93	0.08	Crown cover of <i>Pandanus</i> patch (<25, 25-75, >75%)
Log <i>Pandanus</i> area (m ²)	0.92	0.04	Area of <i>Pandanus</i> (length by width of patch)
Grass cover (index)	3.06	0.06	Percentage grass cover (<5, 5-25, 25-50, 50-75, 75-100%)
Grass height (m)	0.71	0.02	Height of grass
<i>River Structure</i>			
Log river width (m)	1.79	0.02	Width of riparian zone (riverbed plus vegetation)
Log water width (m)	1.25	0.02	Width of water in riverbed
Depth water (index)	2.10	0.04	Depth of water (None, <1m, <2m, >2m)
Sediment size (index)	2.01	0.07	Largest grain size (Sand, gravel, large rocks)
<i>Disturbance</i>			
Weed species richness (index)	0.53	0.05	Number of different weed species (0,1,2,3,4,5+)
Weed cover (index)	1.36	0.04	none, few scattered, 1 patch/several scattered, few patches, many patches, continuous weeds
Signs of cattle (index)	1.79	0.05	Ground with tracks, scats or direct evidence of vegetation damage (<5, 5-25,25%+)
Signs of fire (index)	0.24	0.03	(1) no evidence, 2) old fire scars on tree trunks, 3) recent minor / previous season moderate impact, 4) recent moderate / previous season major impact, 5) recent to channel edge)

Riparian structure

The physical attributes of riparian areas, including location of ground water (Lamontagne *et. al.* 2005; O'Grady *et. al.* 2006), determine patterns of riparian vegetation growth. We measured riparian structure perpendicular to the river bank, and quantified the width of riparian area (the riverbed plus riparian vegetation), the width of water within the riverbed, the depth of water, and the grain size of the sediment (sand, gravel, large rocks).

Disturbance indicators

The major threats to riparian vegetation (and a range of other ecosystems) in the monsoonal tropics of northern Australia are grazing, weeds and mismanaged fire (National Land and Resources Audit 2002; Fisher *et. al.* 2003; Hunt *et. al.* 2007; van Doorn 2007). Within our 10 m survey radius, we measured indicators of cattle presence as the percentage of ground with tracks, scats or other traces of cattle. Evidence of direct vegetation damage by grazing and rubbing were also noted. Weed incursion was quantified by measures of weed species richness (number of weed species) and percentage weed cover. Fire disturbance was quantified by the severity of impact (none, minor, moderate, major) and whether fire had occurred since the end of the last wet-season (recent versus previous seasons). We defined minor impact as grass fires that had some impact on riparian boundary but did not burn mid-storey, moderate impact as fires that burnt grasses and also partly burnt the mid-storey, and major impact when the canopy burnt and/or mid-storey burnt to the edge of the waterway (Table 4.1).

4.3.4. Analysis of habitat requirements

We used data collected from the seven catchment areas where the purple-crowned fairy-wren has ever been recorded (currently occurs and extinct) (Figure 4.1) to construct models of habitat requirements. These models did not include data from catchments where the species has not been recorded because absence from these areas may be unrelated to habitat suitability. To decrease the potential of false negatives, sites designated fairy-wren absent were greater than 100 m distant from sites where the species was detected. Several parameters (*Pandanus* area,

river width and water width) were $\log_{10}$ transformed prior to modelling. All analyses were conducted in GenStat 11.1 (VSN International).

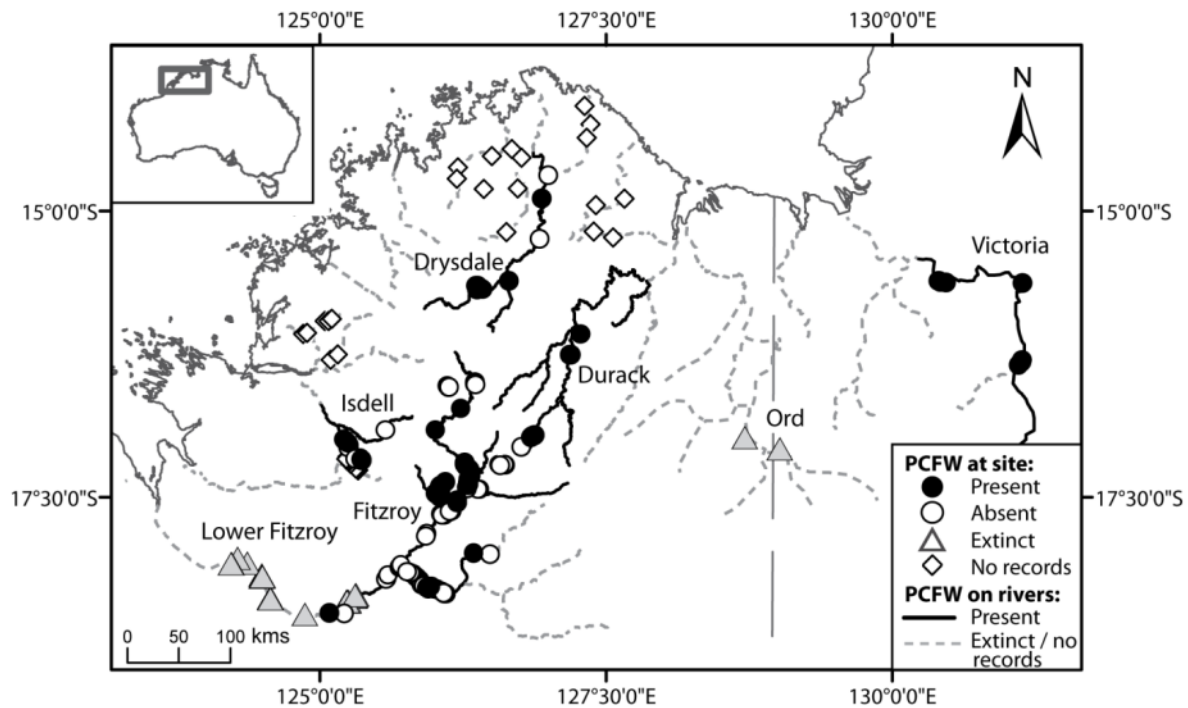


Figure 4.1. Locations where fine-scale habitat attributes were quantified across the distribution of the western purple-crowned fairy-wren. Survey sites were categorized based on occurrence of the species as either (a) present: sites where the species occurs locally, (b) absent: sites without fairy-wrens from sections of catchments where they occur, (c) extinct: sites from sections of catchments where the species was known historically and no longer occurs, or (d) no records: catchments where purple-crowned fairy-wrens have never been recorded. Black lines are rivers where the species is known to occur (present), and dashed grey lines are rivers where the species does not currently occur.

Correlations between habitat attributes were computed prior to modelling. Where high correlation was evident between explanatory variables, we made an *a priori* decision, based on knowledge of habitat use and ecology, to include only one of each pair of correlated variables within a model, and thereby avoid biases from multicollinearity (Graham 2003). We subsequently performed substitutions of highly correlated variables within habitat models to assess the effects of our *a priori* decisions. Although signs of fire were measured during survey

work, we did not include this parameter in analyses due to an extremely low and unbalanced rate of encounter (6% of sites and 5/46 access locations).

As survey sites were spatially clustered around access points to waterways, we employed Generalized Linear Mixed Modelling (GLMM) (McCulloch and Neuhaus 2005), using access points within catchments as a random term to account for spatial clustering (Bolker *et. al.* 2009). We produced three exploratory GLMMs with binomial errors and logit link functions, to investigate the importance of 1) vegetation attributes, 2) river structure, and 3) disturbance on occurrence of purple-crowned fairy-wrens. We produced a fourth GLMM that could be used to predict the probability of purple-crown fairy-wren occurrence at all sites within the study area. Starting with the maximal model containing only uncorrelated parameters, we identified the parameters that had substantial effects on the purple-crowned fairy-wren occurrence using a backward elimination model selection procedure. Model selection was performed in a stepwise manner; with sequential rounds of eliminating the variable with the lowest Wald Statistic and re-fitting the model. The final model is referred to as our “predictive model” and retains only variables that had significant explanatory power ($P < 0.05$).

4.3.5. Model validation

We used cross-validation to assess the reliability of our predictive model to predict occurrence of the purple-crowned fairy-wren (Guisan and Zimmermann 2000; Guisan *et. al.* 2006). K-fold cross-validation was conducted by sequentially excluding data from one of the seven catchment areas where the species had ever been recorded, and re-estimating the parameters in our predictive model using sites from the remaining six areas (n). We used the calibrated model to estimate the predicted probabilities of purple-crowned fairy-wren occurrence for each site within the excluded catchment (Knapp *et. al.* 2003; Wilson *et. al.* 2009). This procedure was repeated seven times, each time excluding a different catchment area. The observed (y) and predicted probabilities ($\hat{y}$) of occurrence for each site were used to compute the misclassification error rate:

$$Error\ rate = \frac{\sum((\hat{y} - y)^2)}{n}$$

and bias:

$$Bias = \frac{\sum(\hat{y} - y)}{n}$$

Individual misclassification error rates for catchments were compared to investigate whether the level of uncertainty in the model varied across the study area.

4.3.6. Prediction of habitat suitability

The predictive model of purple-crowned fairy-wren occurrence was used to investigate whether the suitability of habitat influences the disappearance or absence of the species from several catchments in the Kimberley region. Probabilities of purple-crowned fairy-wren occurrence were generated for each site surveyed, by fitting the logistic regression equation of the predictive model (GLMM):

$$f(y) = a + \beta_1(x_1 - \bar{x}_1) + \beta_2(x_2 - \bar{x}_2) + \beta_3(x_3 - \bar{x}_3) + \dots$$

to the habitat attributes of each site. Probabilities were calculated as values between 0 and 1 (Guisan and Zimmermann 2000) by performing inverse logistic transformation of $f(y)$:

$$P = 1 - \frac{1}{1 + e^{f(y)}}$$

We examined the predictions of purple-crowned fairy-wren occurrence in relation to four categories of sites within the species distribution: (a) sites where the species is present, (b) sites where the species is absent within catchments where they occur elsewhere, (c) sites from sections of catchments where the species is now extinct, and (d) sites within catchments where the species has never been recorded.

4.4. Results

4.4.1. Survey findings

Surveys were conducted at 635 sites across 14 catchments, and the purple-crowned fairy-wren was detected at 96 sites across 5 catchments (Figure 4.1). Of the vegetation the species has a known association with, *Pandanus* was common and encountered at 55% of the 635 sites, however tall river-grasses ($> 1.5\text{m}$) were rare and encountered at only 41 sites (6%). Only 28 sites on the Victoria River and lower to mid Fitzroy contained *Chionachne cyanthopoda*. *Pandanus* was common on most rivers except for the downstream sections of the Victoria and Fitzroy Rivers. Surveys encompassed riparian areas that represented a range of riparian structures from narrow waterways ($< 5\text{ m}$ wide) to anabranching rivers (Wende and Nanson 1998) that were several hundred metres wide.

Impacts of cattle ($> 5\%$ ground affected) were evident at 31% of sites. Fifty-three sites (8%) were severely impacted by cattle, with $> 25\%$ of the ground surface covered in scat and tracks, and riparian vegetation browsed upon. Highly impacted sites were mainly on the lower Fitzroy River, at Drysdale River Crossing and on the Carson catchment, however signs of cattle were common across the study area. Impacts of fire were rarely encountered with only 45 of the 635 sites (7%) showing any signs of fire damage. This may be because we were surveying before the intense fires of the late dry season (Fisher *et al.* 2003; Russell-Smith *et al.* 2003; Legge *et al.* 2011), and it may have been difficult to determine whether fire had occurred in earlier years. Areas that were surveyed shortly after fire were on Bell Creek (Isdell), Wood River (Durack), Hann River crossing (Fitzroy) and the Sale River. Weeds were almost ubiquitous across sites (94%) however a high density of weeds (more than a few scattered patches) was only encountered at 15% of sites. Continuous weed cover was encountered at 18 sites where the purple-crowned fairy-wren is now extinct on the lower Fitzroy and Ord Rivers.

Table 4.2. Correlations between riparian habitat attributes for catchments where purple-crowned fairy-wrens have ever occurred.

Correlation coefficients $r > 0.5$ are displayed in bold. *Pandanus* area, river width and water width were $\log(x+1)$ transformed as in Table 4.1. weed species $\dagger$ = weed species richness; ** $P = <0.001$, * $P = <0.05$; $N = 601$.

Variables	Pearson's correlations (r)													
	Vegetation							River Structure				Disturbance		
	Canopy height	Canopy cover	Shrub density	<i>Pandanus</i> cover	<i>Pandanus</i> area	Grass cover	Grass height	River width	Water width	Water depth	Sediment size	Weed species $\dagger$	Weed cover	Signs of cattle
Canopy cover	0.40**													
Shrub density	0.10*	0.10*												
<i>Pandanus</i> cover	0.28**	0.21**	0.01											
<i>Pandanus</i> area	0.35**	0.27**	-0.12*	0.83**										
Grass cover	-0.05	-0.12*	-0.10*	0.03	0.05									
Grass height	-0.02	0.01	0.01	0.02	0.07	0.59**								
River width	-0.10*	-0.07	0.44**	-0.19**	-0.33**	-0.43**	-0.29**							
Water width	-0.11*	0.00	0.36**	-0.09*	-0.19**	-0.23**	0.04	0.50**						
Water depth	0.00	0.09*	0.16**	0.22**	0.16**	-0.06	0.05	0.02	0.63**					
Sediment size	-0.14**	-0.17**	-0.21**	0.11*	0.15**	0.28**	0.18**	-0.35**	-0.29**	-0.17**				
Weed species $\dagger$	-0.12*	-0.11*	0.15**	-0.31**	-0.36**	0.04	-0.13*	0.34**	0.24**	-0.06	-0.23**			
Weed cover	-0.10*	-0.11*	0.12*	-0.24**	-0.28**	-0.04	-0.08*	0.31**	0.18**	-0.08*	-0.21**	0.80**		
Signs of cattle	0.11*	0.04	-0.02	-0.19**	-0.17**	-0.19**	-0.25**	0.23**	0.16**	-0.11*	-0.31**	0.51**	0.45**	
Fire	0.09*	0.07	-0.14**	-0.03	-0.00	0.01	-0.00	-0.29**	-0.23**	-0.12*	0.09*	-0.11*	-0.10*	-0.15**

4.4.2. Correlations between variates

High levels of correlation ($r \geq 0.5$) were detected between five pairs of predictors (Table 4.2). We made *a priori* decisions to include: 1) *Pandanus* crown cover as it is more reliably measured during survey work than *Pandanus* area ($r = 0.83$; $P < 0.001$), 2) grass height rather than grass cover ($r = 0.59$; $P < 0.001$), as tall grasses are used for nesting (van Doorn and Low Choy 2009), 3) the width of a watercourse, as the width of water within ($r = 0.50$; $P < 0.001$) it is likely to change with season, and 4) weed cover, as it is an indicator of the physical extent of rather than the richness of weed species ($r = 0.8$; $P < 0.001$). Exclusion of these parameters negated the remaining correlation between water width and water depth ($r = 0.63$; $P < 0.001$). No important differences were evident when each correlated variable within a pair was substituted within habitat models. Low, although significant ($P = < 0.001$; $P = < 0.05$), inter-correlations were evident between a number of other habitat variables (Table 4.2)

4.4.3. Habitat requirements

Exploratory data analysis revealed that dense *Pandanus* crown-cover, a well-developed shrub layer and high canopy are the important vegetation predictors of purple-crowned fairy-wren occurrence (Table 4.3). The species is more likely to occur at sites with deep water, with some evidence suggesting wide rivers provide better habitat (Table 4.4). The only important disturbance indicator was signs of cattle which had a marginally negative effect on occurrence (Table 4.5). Of the effects revealed in exploratory analysis, only the significant vegetation effects were retained in the predictive model (Table 4.6). Riparian structure and signs of cattle may therefore be indirect predictors of occurrence.

The cross-validation procedure indicated that the predictive model had a relatively good fit, with an average misclassification rate of 0.2 and low average bias (Table 4.7). However, variation in model fit between catchments was evident (Table 4.7). Although the predictive model performed quite well for five of the catchment areas, it underestimated the probability of purple-crowned fairy-wren occurrence on the Victoria and Drysdale catchments. The high

Table 4.3. The importance of vegetation attributes in explaining the presence of the purple-crowned fairy-wren. Unstandardized partial regression coefficients (β) are listed for variables that significantly ($P < 0.05$) predict occurrence. $N = 601$.

Effects	Predictors	d.f.	F.	P	β	s.e.
Fixed	Constant				-1.502	0.34
	<i>Pandanus</i> crown cover	1, 557.2	40.50	<0.001	0.478	0.075
	Shrub density	1, 506.2	12.50	<0.001	0.288	0.081
	Canopy height	1, 469.3	7.70	0.006	0.081	0.029
	Grass height	1, 380.1	0.20	0.657		
	Canopy cover	1, 583.0	0.32	0.575		
Variance Component					s.e.	
Random	Access point		2.932		1.063	

Table 4.4. The importance of river structure in explaining the presence of the purple-crowned fairy-wren. Unstandardized partial regression coefficients (β) are listed for variables that significantly ($P < 0.05$) predict occurrence. River width and water width on log10 scale. $N = 601$.

Effects	Predictors	d.f.	F.	P	β	s.e.
Fixed	Constant				-1.677	0.360
	Water depth	1, 588.5	7.65	0.006	0.408	0.147
	River width	1, 217.8	3.81	0.052		
	Sediment size	1, 594.0	1.51	0.220		
Variance component					s.e.	
Random	Access point		3.735		1.214	

Table 4.5. The importance of threatening process in explaining the presence of the purple-crowned fairy-wren. Unstandardized partial regression coefficients (β) are listed for variables that significantly ($P < 0.05$) predict occurrence. $N = 601$.

Effects	Predictors	d.f.	F.	P	β	s.e.
Fixed	Constant				-1.694	0.388
	Signs of cattle	1, 356.3	3.73	0.054		
	Weed cover	1, 403.1	1.04	0.308		
Variance Component					s.e.	
Random	Access point		4.319		1.381	

Table 4.6. The predictive model of the importance of habitat parameters for occurrence of the purple-crowned fairy-wren. The predictive model contains only the three vegetation parameters that are significant predictors of occurrence. Unstandardized partial regression coefficients (β) are listed for variables that significantly ($P < 0.05$) predict occurrence. $N = 601$.

Effects	Predictors	d.f.	F.	<i>P</i>	β	s.e.
Fixed	Constant				-1.510	0.345
	<i>Pandanus</i> crown cover	1, 566.1	41.92	<0.001	0.484	0.075
	Shrub density	1, 536.0	14.40	<0.001	0.301	0.079
	Canopy height	1, 450.6	8.78	0.003	0.085	0.029
	Weed cover	1, 278.7	2.25	0.134		
	Signs of cattle	1, 347.1	3.25	0.072		
	Sediment size	1, 587.8	0.91	0.340		
	River width	1, 244.2	0.71	0.400		
	Water depth	1, 570.4	0.19	0.664		
	Grass height	1, 417.3	0.04	0.847		
	Canopy cover	1, 549.9	0.01	0.925		
Variance Component					s.e.	
Random	Access point		3.788		1.308	

misclassification rate for the Victoria River is not unexpected. In this area the species predominantly occurs in river-grass habitat that is not common on the other rivers surveyed. The high error rate for this catchment and general low misclassification rate for other Kimberley rivers (average of 0.12 excluding Victoria) demonstrates that the model performs relatively well for *Pandanus* dominated habitat. The overall negative bias indicates that the model provides a conservative estimate of purple-crowned fairy-wren occurrence.

We compared suitability of habitat between four categories of sites (Figure 4.2) using predictions from the full predictive model based on all sites where the species has ever been recorded. Habitat at sites where the species is now extinct was generally of low suitability, and similar in quality as habitat from unoccupied sites within catchments where the purple-crowned fairy-wren has been recorded elsewhere. This suggests that poor condition of habitat is implicated in the disappearance and continued absence of the species from these areas. In contrast, catchments that have never been known to have purple-crowned fairy-wrens contained

habitat of high suitability (Figure 4.2). This suggests another cause for the absence of purple-crowned fairy-wrens from these catchments.

Table 4.7. Results of the cross-validation procedure assessing the accuracy of the predictive model to predict occurrence of the purple-crowned fairy-wren.

Catchment area	Misclassification rate	Bias
Upper Fitzroy	0.14	0.003
Isdell	0.16	0.032
Durack	0.12	0.000
Drysdale	0.25	-0.180
Ord	0.00	0.000
Victoria	0.65	-0.565
Lower Fitzroy	0.09	0.090
Average	0.20	-0.089

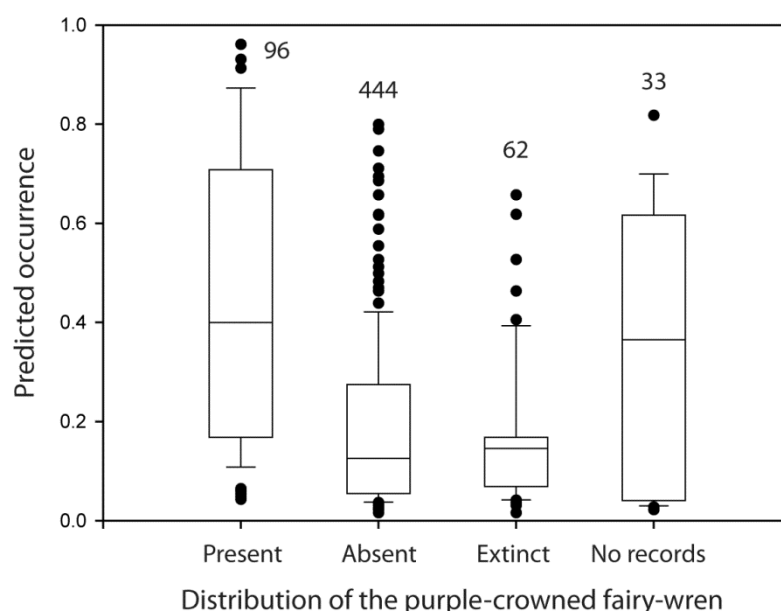


Figure 4.2. The relationship between the predicted occurrence and the distribution of the western purple-crowned fairy-wren. The distribution of the species corresponds with the categories of occurrence in Figure 4.1. Predictions are calculated using the predictive model of habitat requirements (Table 4.6) generated using the 601 present + absent observations. Sample sizes shown above error bars (90% CI).

4.5. Discussion

The distribution of the western purple-crowned fairy-wren is influenced by variation in fine-scale habitat suitability (Figure 4.2). Applying our predictive model of purple-crowned fairy-wren habitat requirements (Table 4.6) to the sites we surveyed suggests that three major processes influence distribution (Figure 4.2). First, the fine-scale quality of local habitat influences the presence of purple-crowned fairy-wrens at sites within catchments where the species currently occurs. Second, a reduction in fine-scale habitat quality along stretches of waterways has caused both the recent disappearance of the species from the Ord River (Skroblin and Legge 2010), and the continued absence of the species from parts of its former range (Rowley 1993; Skroblin and Legge 2010). Finally unmeasured variables, such as landscape arrangement or context (i.e. Martin *et. al.* 2006; Prugh *et al.* 2008; Wilson *et. al.* 2009; Gray *et. al.* 2010), may prohibit the occurrence of the purple-crowned fairy-wren within catchments where we identified suitable habitat but the species has never been recorded.

4.5.1. Fine-scale habitat requirements

Along catchments where the purple-crowned fairy-wren occurs, the presence of the species at a particular site is highly dependent on fine-scale habitat suitability. Habitat that is suitable for the fairy-wren contains two important vegetation structures: firstly a dense mid-storey comprised of *Pandanus* and/or shrubs (or grasses), and secondly a tall canopy of emergent trees often dominated by *Eucalyptus camaldulensis*, *Melaleuca leucadendra*, *Melaleuca argentea* and *Ficus* spp. (Tables 4.3 & 4.6). A dense mid-storey provides foraging and nesting opportunities (Rowley and Russell 1993; Kingma *et. al.* 2010), as well as shelter from predators (Rowley and Russell 1997), while a tall canopy provides refuge during flooding events that submerge the mid-storey (Rowley and Russell 1993; A. van Doorn unpublished data, 2008; M. Hall, unpublished data, 2009).

During our survey, we located purple-crowned fairy-wrens in areas that contained various combinations of mid-storey plants. The association of the species with *Pandanus* spp. or

river grass is consistent with earlier observations (Wheeler 1965; Boekel 1979; Rowley 1993; Rowley and Russell 1993; van Doorn 2007), however the importance of dense shrubs (Tables 4.3 & 4.6) has not been previously noted. We detected three territories where the mid-storey was comprised primarily of freshwater mangroves (*Barringtonia acutangula*) that lacked *Pandanus aquaticus* and river grasses. Although nesting has primarily been recorded in river grass (van Doorn 2007) and *Pandanus aquaticus* (Rowley and Russell 1993; Kingma *et al.* 2010), the occasional observation of nests built in freshwater mangroves (M. Hall, unpublished data, 2010), suggests such territories may be suitable. We further emphasise the importance of a tall canopy structure (Rowley 1993; van Doorn 2007), as the species was never located in areas lacking emergent trees and was often observed foraging and conducting territorial duets high in the canopy.

The occurrence of the purple-crowned fairy-wren was also associated with the physical structure of riparian areas (Table 4.4). Although not included within the predictive model of occurrence (Table 4.6), the depth of water significantly and the width of waterway marginally predicted occurrence in the exploratory analysis. This suggests that riparian structure influences the growth of vegetation that is important for the species, probably by allowing access to ground water (Lamontagne *et al.* 2005).

4.5.2. Distribution of habitat types

Descriptions of the ecology of the purple-crowned fairy-wren are complicated by the strong affinity of the species with two very different vegetation types; *Pandanus aquaticus* and *Chionachne cyanthopoda*. While *Pandanus* was relatively common in the areas we surveyed, tall grasses were rare and only a few sites contained *Chionachne cyanthopoda*. Due to the predominance of *Pandanus* type habitat in our study area, we failed to identify grass height as an important predictor of purple-crowned fairy-wren occurrence. Consequently our model displayed poor ability to predict occurrence of the purple-crowned fairy-wren in the Victoria catchment which is dominated by river-grass habitat (Table 4.7). This difference in habitat

requirements strengthens the need for site-specific management (van Doorn 2007) that is tailored towards the dominant habitat type.

4.5.3. *Habitat degradation and population persistence*

The current distribution of the purple-crowned fairy-wren appears to be strongly influenced by patterns of riparian degradation within the species range. Habitat along the lower Fitzroy and Ord Rivers, where the species has disappeared (Smith and Johnstone 1977; Rowley 1993; Skroblin and Legge 2010), is lower in quality than other areas where the species still occurs. The low probability of occurrence for these areas corresponds with the deficiency of understorey structure, while the abundant signs of cattle and profuse growth of weeds attest to the continuing degradation.

Over-grazing by introduced herbivores has previously been thought to have influenced the declines of the purple-crowned fairy-wren (Smith and Johnstone 1977; Rowley 1993; Garnett and Crowley 2000; van Doorn 2007). Grazing, by modifying the structural complexity of habitat, has been implicated in changes in riparian bird assemblages (Krueper *et al.* 2003; Scott *et al.* 2003), and especially impacts on birds that utilize the riparian understorey (Jansen and Robertson 2001; Martin and Possingham 2005; Lees and Peres 2008). The major impact of cattle grazing, which appears to be an indirect predictor of purple-crowned fairy-wren occurrence, may be the reduction in the shrub-layer which the species relies on for nesting, foraging and shelter. This appears to be particularly the case for the lower Fitzroy River where river-grass habitat remains sparse and abundant signs of cattle suggest a high continuing grazing. High intensity grazing can rapidly decrease the height of *Chionachne cyanthopoda* and result in alarmingly high rates of adult mortality and associated decreases in breeding success of purple-crowned fairy-wrens (van Doorn 2007). Similar processes may occur in intensely grazed sites containing *Pandanus* type habitat, as we encountered sites where the foliage was completely absent up to a level that could be reached by grazing cattle and purple-crowned fairy-wrens were not detected.

Although fire was rarely encountered during our survey, the potential ecological impact of fire on riparian habitat can be severe. Intense fire reduces the density of woody plants and diversity of riparian tree species (Andersen *et al.* 2005), and bird species such as the purple-crowned fairy-wren that forage or nest in shrubby understorey may decline after burning if their resources have been adversely affected (Artman *et al.* 2001; Valentine *et al.* 2007). We never detected purple-crowned fairy-wrens at sites where the understorey had been severely impacted by fire, but did locate the species at sites where the grass understorey had burnt and the shrubby mid-storey vegetation had been minimally affected. Implementation of the current management focus on early dry season burning, which reduces the extent of more intense late season burns (Craig 1997; Yates *et al.* 2008; Legge *et al.* 2011), will help to protect riparian habitat.

4.5.4. *Unexplained variation in distribution*

In addition to the strong influence of fine-scale habitat attributes on distribution, our findings also suggest that unmeasured variables, such as those operating at other scales (Smith and Hellmann 2002; Betts *et al.* 2007), may also influence the distribution of the purple-crowned fairy-wren. Based on the parameters measured in this study, suitable habitat for the species was detected on several rivers in the Kimberley region where the species has never been recorded, and in small amounts in areas where the species is currently extinct. Failure of the species to inhabit these areas suggests there may be thresholds in dispersal capabilities or patterns of habitat fragmentation that predict occurrence (Fahrig 2001; Radford and Bennett 2003; Betts *et al.* 2007). Alternatively, absence from suitable habitat may indicate the population is below carrying capacity (Thompson Hobbs and Hanley 1990), or that our model did not account for all important fine-scale habitat predictors. An assessment of landscape-scale influences on occurrence may further explain the distribution of the western purple-crowned fairy-wren.

4.5.5. *Implications*

The declining condition of riparian habitat in northern Australia (National Land and Resources Audit 2002) has resulted in contractions in the distribution of the purple-crowned

fairy-wren. The reliance of the species on dense understorey increases its vulnerability to negative impacts of grazing (Martin and Possingham 2005), and fire (Valentine *et al.* 2007) which decrease the density of understorey shrubs (Andersen *et al.* 2005; Lees and Peres 2008). To conserve this species, and maintain the rich and varied biodiversity of the riparian ecosystems in northern Australia (Russell-Smith 1991; Woinarski *et al.* 2000), it is vital to halt the decline in the condition of riparian habitat. For avian specialists of the riparian understorey, condition of habitat and thus abundance and species richness (Martin and McIntyre 2007; Nelson *et al.* 2011) may be best enhanced by managing grazing and fire to preserve the structural complexity of the shrub-layer (Lees and Peres 2008). In northern Australia, where large scale fencing is often unfeasible (Hunt *et al.* 2007), grazing pressure on riparian areas may be reduced by decreasing stocking rates or by provisioning water points away from riparian areas (Jansen and Robertson 2001). The integrity of the understorey will be further enhanced through implementation of early dry season burning to reduce the extent of more intense late season burns (Craig 1997; Yates *et al.* 2008; Legge *et al.* 2011).

To halt declines in the condition of riparian habitat in northern Australia (National Land and Resources Audit 2002), some conservation effort should be directed to preserving the quality of riparian habitat that is currently the least degraded. Due to its sensitivity to understorey degradation, the purple-crowned fairy-wren may be an indicator (Cairns *et al.* 1993) of the condition of riparian vegetation on those rivers where it occurs. The differences in the species ecology between *Pandanus* and river-grass habitat (Rowley 1993; van Doorn 2007) identifies the need for riparian management that accounts for site-specific differences in vegetation. Conservation effort to maintain the complexity of the understorey and connectivity between riparian areas of high condition will help to ensure persistence of riparian habitat specialists in northern Australia.

CHAPTER 5

Up the creek without a paddle: the population genetics of the purple-crowned fairy-wren, a declining riparian passerine

Authors: Anja Skroblin, Andrew Cockburn and Sarah Legge

Format: Conservation Genetics



Female purple-crowned fairy-wren

© Anja Skroblin

5.1. Abstract

We investigate the population genetic structure of the declining western subspecies of the purple-crowned fairy-wren, *Malurus coronatus coronatus*, to guide conservation management directives for this riparian habitat specialist. Our analysis of multi-locus microsatellite data, from 79 individuals sampled from across the species' range, indicates that *M. c. coronatus* occurs as genetically divergent subpopulations that correspond to catchment boundaries or expansive gaps in habitat along waterways. The genetic similarity of three large populations (Fitzroy, Durack and Victoria) may indicate substantial historical gene flow, whereas the high genetic distinctiveness of the Bindoola, Isdell and Drysdale catchments reflect the current geographic isolation of these small populations. Genetic divergence and isolation of these small populations and a subpopulation on the Victoria river affirms the negative effect habitat degradation and fragmentation has had on population connectivity. If current management practices are to continue, we can expect that increasing isolation and contraction of populations will compound with an increased risk of extinction.

5.2. Introduction

Species occurring in patchily distributed habitat may occur as partially isolated subpopulations connected by differing levels of dispersal (Fahrig and Merriam 1994; Hanski 1998). For such species, knowledge of population connectivity may be particularly important in guiding management directives for conservation (Soulé *et. al.* 2006). It may also provide insights into the potential genetic consequences that future degradation and fragmentation of habitat may have on gene flow (Dieckmann *et. al.* 1999; Gerlach and Musolf 2000; Coulon *et al.* 2010).

For species that occur in patchily distributed habitat, the geographic distribution of neutral genetic diversity reveals important information on current population dynamics and historical patterns of gene exchange (Charlesworth *et. al.* 2003). Patterns of genetic diversity within subdivided populations can help guide conservation management to maintain viable populations

that retain their genetic diversity, and hence their evolutionary potential and resilience to environmental stochasticity (Frankham 1995; Amos and Balmford 2001; Moritz 2002). This can be achieved by optimizing the size of subpopulations to prevent inbreeding and ameliorate genetic drift (Frankham 1996), and by maximising connectivity, which can be influenced by the life-history traits of species (Dieckmann *et al.* 1999; Aars *et al.* 2006), geographic isolation of habitat (Manel *et al.* 2003), patterns of fragmentation (Travis and Dytham 1999) or suitability of the matrix (Ricketts 2001). As habitat is lost and populations are fragmented, understanding of landscape connectivity is important to prevent declines in persistence associated with reduced dispersal success (King and With 2002) and negative genetic effects such as inbreeding depression and reduced evolutionary potential (Crandall *et al.* 2000; Spielman *et al.* 2004).

A species for which knowledge of population genetic structure would improve conservation management is the patchily distributed purple-crowned fairy-wren (*Malurus coronatus*). The purple-crowned fairy-wren is a small passerine that is restricted to naturally constrained and narrow patches of riparian vegetation that are distributed along waterways within the tropical savannahs of northern Australia (Higgins *et al.* 2001; Barrett *et al.* 2003). As this species is reliant on a dense understorey (Skroblin and Legge 2011) its habitat is sensitive to degradation and fragmentation through increased frequency of intense fires (Woinarski 1990; Valentine *et al.* 2007), grazing by introduced herbivores (Rowley 1993; van Doorn 2007; Skroblin and Legge 2011) and associated weed incursion (McKenzie *et al.* 2009).

The western subspecies, *Malurus coronatus coronatus*, which is the focus of the present paper, has been particularly susceptible to these factors. Based on recent declines in both range and abundance, and extinction from some river catchments in which it was previously recorded (Smith and Johnstone 1977; Rowley 1993; van Doorn 2007; Skroblin and Legge 2010), it has recently been accorded conservation status of endangered (Garnett *et al.* 2010). The increased isolation and reduced size of extant populations is likely to disrupt dispersal patterns and enhance genetic division within *M. c. coronatus* (eg. Funk *et al.* 2005; Zellmer and Knowles

2009), thus exposing remnant populations to higher risk of extinction (Pimm *et al.* 1988; Fahrig 2001)

Knowledge of the population genetic structure of *M. c. coronatus* is clearly needed to improve conservation management and halt the continued declines of this fairy-wren. In the absence of genetic information, and based on the documented limited dispersal capability in this species (Rowley and Russell 1993), it has been proposed that each catchment containing *M. c. coronatus* could be considered to contain a subpopulation for the purpose of conservation management (Skroblin and Legge 2010). This approach to conservation, however, may be misinformed if population structure inferred from assumed dispersal behaviour does not match the underlying genetic structure (Slatkin 1985; Bohonak 1999; Yu *et al.* 2010).

Here we assess the population genetic structure within and among the extant populations of *M. c. coronatus* the endangered western subspecies of the purple-crowned fairy-wren. We test the hypothesis that each catchment within the range of *M. c. coronatus* contains a separate subpopulation of the purple-crowned fairy-wren using two methods: (i) Analysis of Molecular Variance (AMOVA), a procedure which partitions genetic variance among and between predetermined populations, and (ii) the Bayesian clustering program STRUCTURE, which identifies genetic clusters based on genotypic frequencies without presuming *a priori* population structure. The findings will help direct conservation management by describing the dispersal patterns, as well as, the demographic and genetic threats faced by remnant populations

5.3. Methods

5.3.1. Sampling design

Blood samples were attained from 79 *M. c. coronatus* across the six catchments where the species currently occurs (Skroblin and Legge 2010). To investigate the influence that landscape features within catchments have on genetic structure, individuals were sampled from multiple locations within catchments when accessibility allowed (Figure 5.1). The extent of sampling

within each catchment reflected the size of the catchment and the number of locations at which populations were encountered during survey. We aimed to sample approximately 15 non-related individuals from each catchment if possible, but were unable to do so for the Bindoola catchment where only four territories were detected.

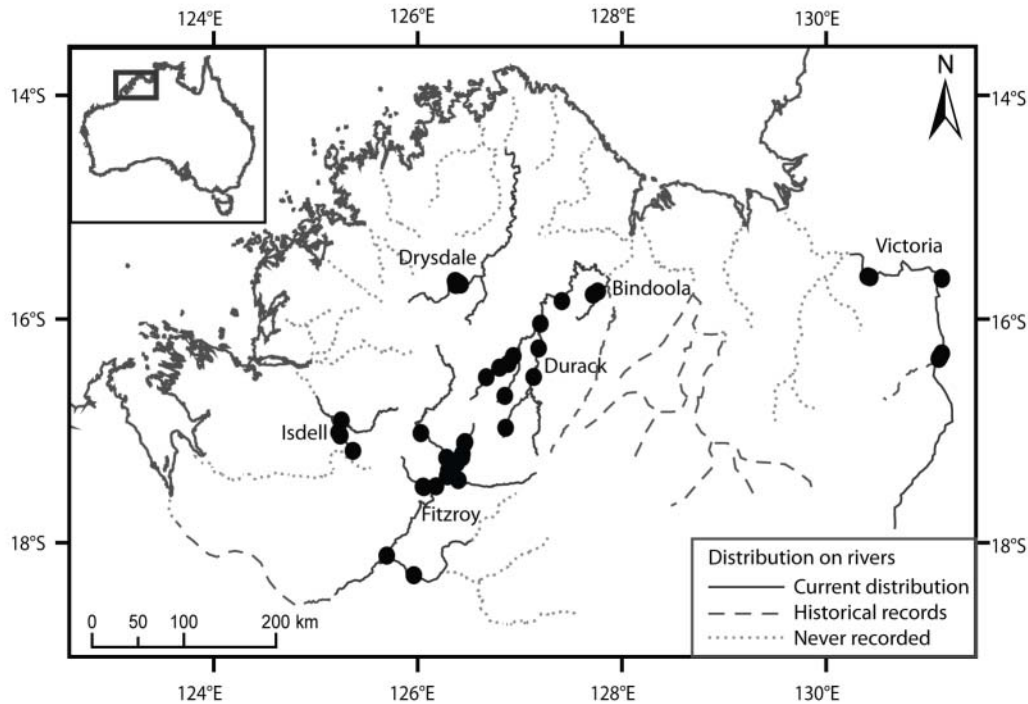


Figure 5.1. Locations where *M. c. coronatus* was sampled for genotyping (N= 79). River names designate the six catchments containing remnant populations. Note that there have been recent extinctions from the river catchment between Bindoola and Victoria. Information on occurrence on rivers modified from Skroblin and Legge (2010).

Surveys for purple-crowned fairy-wrens were conducted following Skroblin and Legge (2010). For each territorial group that was encountered, we attempted to sample only the dominant male and female. Blood samples were however collected from sub-ordinates, which are usually the progeny of the territorial pair (Kingma *et al.* 2009), when the dominant individuals in a group could not be captured. For a group, samples from either the territorial pair or from sub-ordinates were included in the analysis, but this should not bias results as full-sib incestuous pairings within this subspecies is limited (Kingma *et al.* 2009), and natal dispersal of

females is on average further than that of males (M. Hall unpublished data). Each bird was given a unique leg band to prevent re-sampling before being released. Upon collection blood samples were either stored immediately in 70% ethanol or on Whatman FTA® cards (Whatmans). The location of each sampled group was recorded using a handheld GPS (Garmin GPSmap 60, Schaffhausen, Switzerland).

5.3.2. DNA extraction and genotyping

Each individual was genotyped at seven microsatellite loci, six of which have been previously used for paternity assignment in *M. c. coronatus* (Kingma *et al.* 2009). Loci were derived by cross-species amplification from the superb fairy-wren (*Malurus cyaneus*): Mcyu1, Mcyu3, Mcyu4, Mcyu8 (Double *et al.* 1997), the splendid fairy-wren (*Malurus splendens*): Msp4, Msp6 (Webster *et al.* 2004) and the grey-crowned babbler (*Pomatostomus temporalis*): Pte24 (Blackmore *et al.* 2006).

Total genomic DNA was extracted from blood samples stored in 70% ethanol using a conventional proteinase K, ammonium acetate and ethanol protocol. A lambda mass standard was used to approximate the concentration of DNA via electrophoresis in a 2% agarose gel that was post-stained with gel red and visualized under UV light. DNA was diluted to an approximate concentration of 20 ng / ml. Blood stored on Whatman FTA® cards was eluted from a 2 mm diameter circular punch of card using a methanol fixation method (Johanson *et al.* 2009). Eluted DNA was not diluted and used in PCR reactions within 48 hours of elution.

Microsatellite loci were amplified in separate PCR reactions. The 20 µL reaction volumes contained 1.0 µL of template DNA, 2.0 µL of 10x PCR buffer (Qiagen), 1.2 µL of 50 mM MgCl₂, 0.5 µL 1x BSA (Qiagen), 2.0 µL dNTPs (10mM), 0.3 µL M13-tagged forward primer (2 pmol/µL), 2.0 µL of each the reverse primer and the fluorescent labelled M13-tag (2 pmol/µL), 9.9 µL of double distilled H₂O, and 1 unit of Taq (Qiagen). The amplification procedure used was 3 min at 94°C, 35 cycles of 30 s at 94°C, 30 s at 55°C and 30 s at 72°C. The final extension was 4 min at 72°C.

PCR products underwent a clean-up procedure prior to visualization of microsatellite variation. 1 μL of the amplified PCR product was precipitated in a mixture of 3 μL NaAc (3M), 10 μL double distilled H_2O and 41 μL 100% ethanol. Samples were incubated at room temperature for 30 mins, followed by 30mins of centrifuging at 4000 rpm before the supernatant was discarded. To remove salts, samples were centrifuged at 4000 rpm for 10 mins in 80 μL ethanol (70%). This process was repeated three times, with ethanol discarded between washes, before samples were allowed to air dry at room temperature. The cleaned PCR products were resuspended in 18.95 μL of Hi-Di™ Formamide with 0.05 μL of GeneScan™ 500 LIZ™ Size Standard (Applied Biosystems). Genotypes were determined on a 3130x1 Genetic Analyser using GeneScan® Analysis Software and GeneMapper® 3.7 (Applied Biosystems).

5.3.3. Genetic diversity

We investigated overall patterns of genetic diversity by calculating the number of different alleles (N_a), the Fixation Index (F_{IS}), and the observed (H_o) and expected (H_e) heterozygosity for each locus and population. Each locus was tested for conformity to Hardy-Weinberg expectations of genotypic frequencies. Micro-checker v 2.2.3 (Van Oosterhout *et. al.* 2004) was used to test for evidence of scoring error due to stuttering, large allele dropout, or null alleles.

5.3.4. Population Genetic structure

To investigate the partitioning of genetic variation within and between catchments we employed Analysis of Molecular Variance (AMOVA) in GenAlEx 6.4 (Peakall and Smouse 2006) running 999 permutations for significance testing. Pairwise Φ_{PT} values, the proportion of the total variance that is among populations, were calculated to estimate divergence between the six catchment groups we sampled. Divergences between populations were visualized using Principal Coordinates Analysis (PCA) using the covariance matrix. We also conducted a Mantel test to test for isolation-by-distance. The test was carried out using a matrix of pairwise Φ_{PT} values between catchments and geographical distance as measured in Euclidean distance between the centre of catchment populations.

We further investigated population genetic structure using STRUCTURE 2.3.3 (Pritchard *et al.* 2000), a program which constructs genetic clusters based on genotypic frequencies rather than *a priori* knowledge of geographic information. STRUCTURE uses a Bayesian Markov chain Monte Carlo (MCMC) method that uses the assumption of Hardy-Weinberg and linkage equilibrium within subpopulations to find the number of genetic clusters (K), based on the likelihood of individual's genotypes belonging to these genetic clusters (Pearse and Crandall 2004). We implemented the 'admixture model' with 'correlated allele frequencies' (Falush *et al.* 2003). Due to the limited number of samples collected per catchment, we used the catchment location of samples as a prior within the model (Hubisz *et al.* 2009), which strengthened the ability of the model to detect weak patterns but did not bias the model to detecting spurious structure when there was none (Hubisz *et al.* 2009). We conducted five independent runs of models with cluster number (K) ranging from 1 to 10 with a burn-in period of 50 000 MCMC iterations and 100 000 sampling iterations. The most likely K was evaluated using $\ln Pr(X|K)$; the mean log-likelihood that the genotypes sampled (X) belong to K clusters (Pritchard *et al.* 2000), and ΔK ; a quantity based on the rate of change in the log-likelihood between successive K values (Evanno *et al.* 2005).

5.4. Results

5.4.1. Genetic diversity

The Micro-checker v2.2.3 (Van Oosterhout *et al.* 2004) analysis failed to reveal any evidence of scoring error due to stuttering, large allele dropout or null alleles. Seventy-nine alleles were detected for seven microsatellite loci in six populations (total 79 individuals). Heterozygosity of loci within populations ranged from 0.00 – 1.00 (observed and expected). Three departures from Hardy-Weinberg equilibrium were detected, the locus *Pte24* in two populations and *Mcyu1* in a single population. In both cases there was a deficiency of heterozygotes.

Table 5.1. Genetic diversity of seven microsatellite markers across six sub-populations of *M. c. coronatus*.

Estimates are for each locus and across loci within each sub-population population for number of alleles (N_a); the inbreeding coefficient within individuals relative to the subpopulation (F_{IS}); Shannon's index (I); observed (H_o) and expected (H_e) heterozygosity; difference ($p < 0.05 = *$) from Hardy-Weinberg expectations of genotypic frequencies (HWE).

Locus	Bindoola ($N = 7$)					Drysdale ($N = 15$)				
	N_a	H_o	H_e	F_{IS}	HWE	N_a	H_o	H_e	F_{IS}	HWE
Mcyu1	3	0.67	0.67	0.00	0.11	6	0.57	0.60	0.05	0.01*
Mcyu3	3	0.71	0.65	-0.09	0.52	9	0.67	0.83	0.20	0.29
Mcyu4	2	0.29	0.24	-0.17	0.66	2	0.47	0.42	-0.11	0.67
Mcyu8	7	0.86	0.82	-0.05	0.61	10	1.00	0.86	-0.16	0.74
Msp4	3	0.71	0.56	-0.27	0.64	5	0.67	0.63	-0.06	0.92
Msp6	3	0.29	0.26	-0.12	0.98	6	0.87	0.78	-0.10	0.79
Pte24	1	0.00	0.00	-	-	2	0.40	0.48	0.17	0.52
Mean	3.1	0.50	0.46	-0.12		5.7	0.66	0.66	0.00	
SE	0.7	0.12	0.11	0.04		1.2	0.08	0.07	0.05	

Locus	Durack ($N = 15$)					Fitzroy ($N = 15$)				
	N_a	H_o	H_e	F_{IS}	HWE	N_a	H_o	H_e	F_{IS}	HWE
Mcyu1	5	0.70	0.68	-0.04	0.26	8	0.90	0.85	-0.07	0.18
Mcyu3	6	0.54	0.72	0.25	0.12	10	0.87	0.84	-0.03	0.08
Mcyu4	2	0.67	0.50	-0.34	0.19	2	0.40	0.44	0.10	0.70
Mcyu8	13	0.93	0.91	-0.03	0.26	13	0.79	0.89	0.12	0.82
Msp4	9	0.79	0.76	-0.03	0.94	7	0.53	0.57	0.07	0.97
Msp6	6	0.73	0.80	0.08	0.55	5	0.85	0.74	-0.14	0.94
Pte24	3	0.20	0.57	0.65	0.00*	4	0.36	0.58	0.38	0.05
Mean	6.3	0.65	0.70	0.08		7	0.67	0.70	0.06	
SE	1.4	0.09	0.05	0.12		1.4	0.09	0.06	0.06	

Locus	Isdell ($N = 13$)					Victoria ($N = 14$)				
	N_a	H_o	H_e	F_{IS}	HWE	N_a	H_o	H_e	F_{IS}	HWE
Mcyu1	3	0.55	0.48	-0.13	0.81	4	0.78	0.56	-0.38	0.72
Mcyu3	5	0.80	0.74	-0.08	0.62	8	0.58	0.80	0.27	0.05
Mcyu4	2	0.46	0.50	0.07	0.80	2	0.46	0.36	-0.30	0.28
Mcyu8	7	0.58	0.74	0.21	0.12	13	0.85	0.88	0.04	0.32
Msp4	1	0.00	0.00	-	-	5	0.42	0.60	0.30	0.20
Msp6	4	0.77	0.60	-0.28	0.60	6	0.62	0.72	0.14	0.08
Pte24	5	0.62	0.74	0.17	0.24	4	0.33	0.67	0.50	0.04*
Mean	3.8	0.54	0.54	-0.01		6	0.58	0.65	0.08	
SE	0.8	0.10	0.10	0.07		1.3	0.07	0.06	0.12	

Population wide inbreeding coefficients were close to zero for all populations, suggesting that mating is close to random, with no evidence of either negative or positive assortative mating (Table 5.1).

5.4.2. Population genetic structure

The genetic variance between populations occurring in six different catchments was quantified using AMOVA (Table 5.2). Although the majority of variance occurred within catchments (87%), subdivision between catchments was substantial (13%, $\Phi_{PT} = 0.132$, $p \leq 0.001$). Levels of differentiation between catchments, as measured by pairwise Φ_{PT} , were significant between all catchments ($p < 0.05$), with pairwise differences ranging from $\Phi_{PT} = 0.04$ to $\Phi_{PT} = 0.33$ (Table 5.3). Bindoola was the most divergent catchment, and it had the highest pairwise Φ_{PT} differences to the other catchments (all > 0.168 and significant at $p < 0.001$). The Isdell catchment was the second most divergent from the other catchments with slightly lower pairwise Φ_{PT} differences (all > 0.11 and significant at $p < 0.001$). Principal Coordinates Analysis of Φ_{PT} differences (Figure 5.2) further emphasized the genetic divergence of the Bindoola, Isdell and also the Drysdale catchment, and the low genetic divergence between the Fitzroy and Durack catchments. The analysis suggests there is little genetic variance among the Victoria, Fitzroy and Durack catchments. We did not detect a signal of Euclidean isolation-by-distance between catchments using pairwise Φ_{PT} differences (Figure 5.3).

Table 5.2. Partitioning of genetic variation within and among catchments using AMOVA. The Φ_{PT} - statistic is the fraction of the total variance that is among populations.

Source of Variation	df	SS	MS	Variance	% Var.	Φ_{PT} - Statistic	Probability
Among catchments	5	87.7	17.55	0.89	13	0.132	0.001
Within catchments	73	428.8	5.87	5.87	87		
Total	78	516.5		6.77	100		

Table 5.3. Pairwise Φ PT differences between catchments calculated using AMOVA. Probability values were calculated using 999 random permutations of Φ PT and shown above the diagonal. Φ PT = the fraction of the total variance that is among populations.

	Bindoola	Drysdale	Durack	Fitzroy	Isdell	Victoria
Bindoola	-	0.001	0.001	0.001	0.001	0.001
Drysdale	0.332	-	0.004	0.001	0.001	0.001
Durack	0.218	0.075	-	0.014	0.001	0.021
Fitzroy	0.225	0.118	0.044	-	0.001	0.045
Isdell	0.326	0.231	0.109	0.124	-	0.001
Victoria	0.168	0.127	0.047	0.041	0.097	-

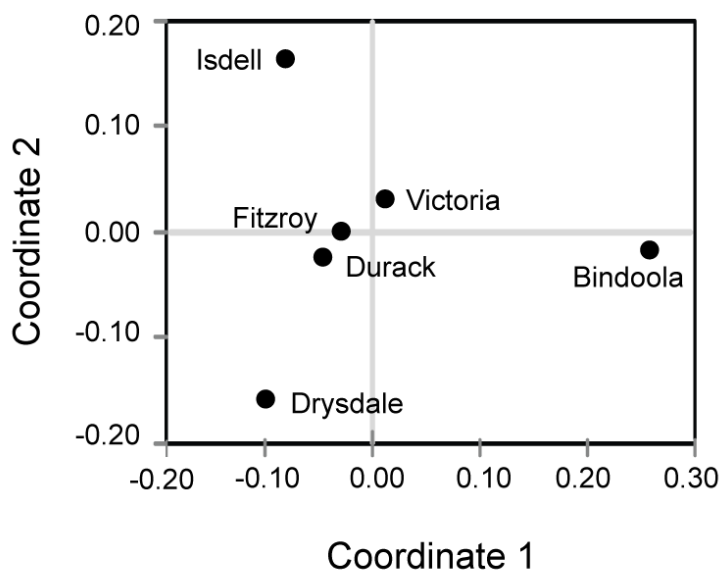


Figure 5.2. Principal Coordinates Analysis of Φ PT differences between catchment populations of purple-crowned fairy-wrens. Coordinate 1 accounts for 50.1% and coordinate 2 for 30.9% of the variation (total 81%).

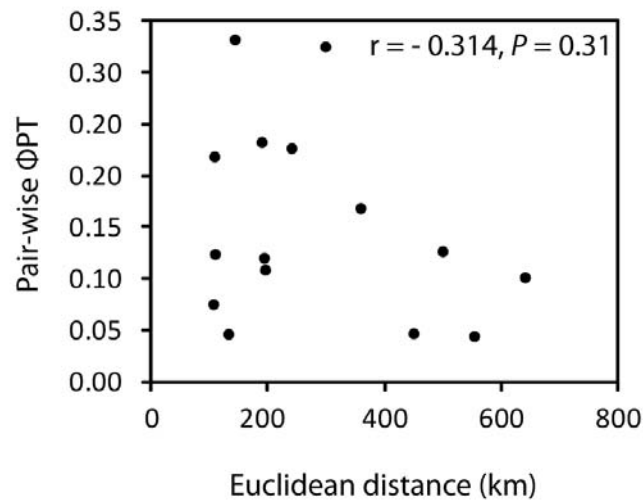


Figure 5.3. Relationship between pairwise Φ_{PT} values and geographical distance as measured in Euclidean distance between catchment populations. Mantel test of isolation by distance: $r = -0.31$, $P = 0.31$.

Genetic differentiation between catchments was supported by Bayesian structure analysis using STRUCTURE 2.2.3. We used two methods of evaluating the number of clusters: $\ln Pr(X|K)$ (Pritchard *et al.* 2000) and ΔK (Evanno *et al.* 2005), both of which suggested the presence of five genetic clusters of *M. c. coronatus* (Figure 5.4). Fairy-wrens from each of four catchments (Bindoola, Drysdale, Fitzroy, and Isdell) had a high probability of assignment to a genetic cluster associated with that single catchment. The Durack and Victoria catchments however had heterogeneous assignments. Fairy-wrens within the Durack catchment had a high and equal probability of membership into the genetic clusters that were associated with the Fitzroy and Drysdale catchments, and lower probability of assignment to the other three clusters. The fifth genetic cluster appeared within the Victoria catchment (Figure 5.5). Individuals from one sampling location on the Victoria River, Big Horse Creek, were identified as belonging to this fifth cluster. Individuals from two other locations, Victoria River Bridge and Dashwood Crossing, showed a high probability of membership to the genetic cluster associated with the Fitzroy, catchment and a lower probability of assignment to the Big Horse Creek and Bindoola clusters.

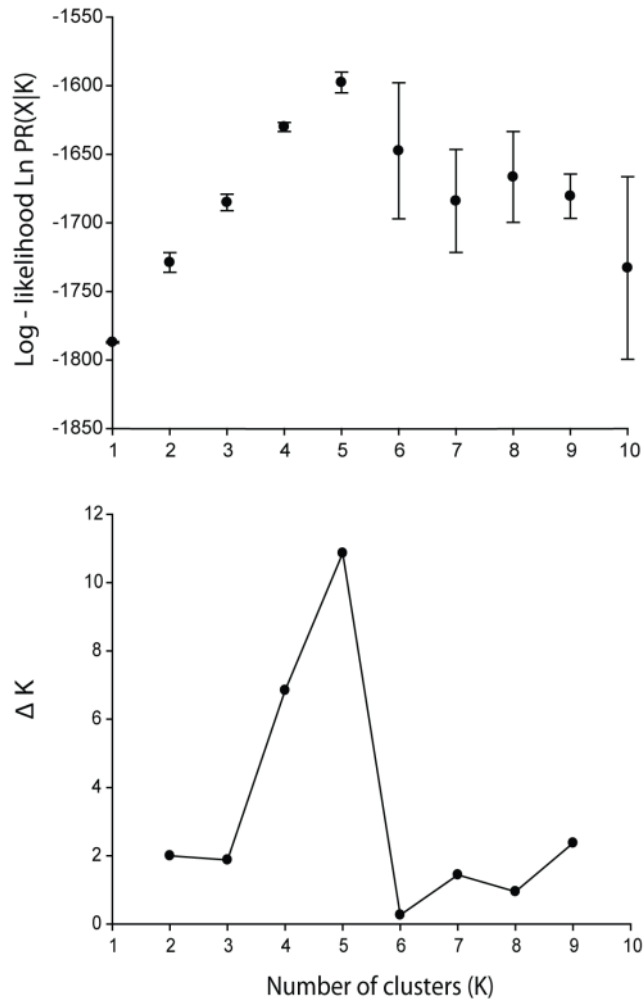


Figure 5.4. Estimated number of genetic clusters of *M. c. coronatus* from Bayesian structure analysis using the program STRUCTURE 2.2.3. Two methods of evaluating the number of clusters were utilized: A) Mean log-likelihood ($\pm$ SD) of different numbers of clusters (K) (Pritchard *et al.* 2000), error bars denote standard deviations, and. B) ΔK values, a quantity based on the rate of change in the log-likelihood between successive K values (Evanno *et al.* 2005), for different numbers of clusters.

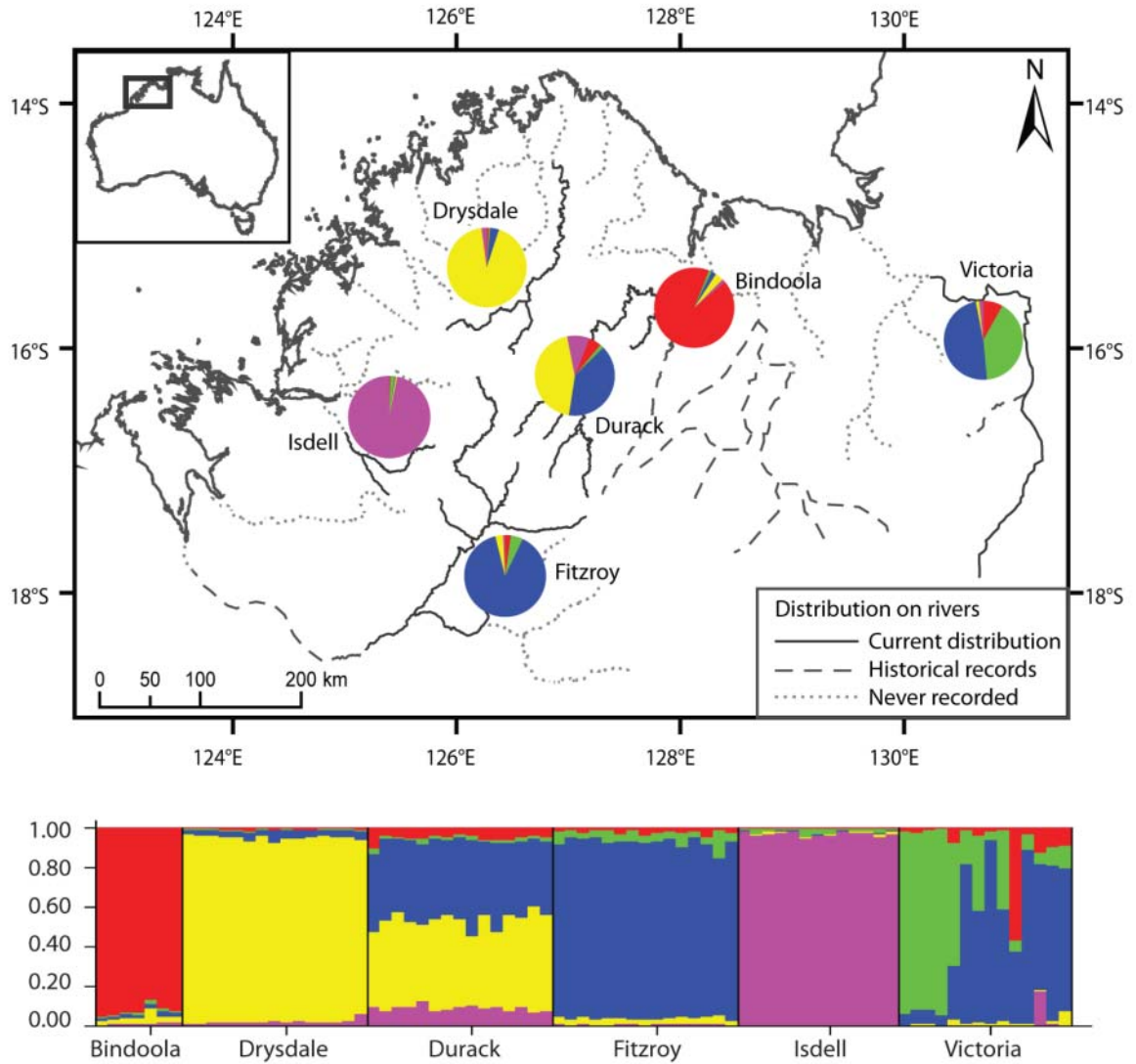


Figure 5.5. Results of the Bayesian structure analysis using the program STRUCTURE 2.2.3. A) The pie charts represent the mean membership fraction of populations within each catchment to the five genetic clusters. B) Individual assignment probabilities to 5 genetic clusters (K) for purple-crowned fairy-wrens from six catchments. Individuals are represented by thin vertical lines which are apportioned into coloured segments that represent the individual's probability of membership into each of the five genetic clusters.

5.5. Discussion

Knowledge of the population genetic structure of the western purple-crowned fairy-wren, *M. c. coronatus*, is important to direct conservation management of this endangered species. Our analysis reveals that *M. c. coronatus* occurs as genetically divergent subpopulations that correspond to catchment boundaries or expansive gaps in habitat along waterways (Table 5.2 & 5.3; Figure 5.5). The three largest populations were most genetically similar regardless of geographic proximity, while the most genetically divergent populations were those that were small and/or isolated. The striking signals of local isolation and genetic differentiation of subpopulations that have been impacted by recent habitat degradation suggests that if current land management practices are to continue we can expect these processes to compound with increased risk of extinction.

5.5.1. Population genetic structure

Genetic structure of *M. c. coronatus* appears to be a function of geographic connectivity of habitat both along waterways, and between catchments. Although purple-crowned fairy-wrens were thought to be relatively poor dispersers based on behavioural observations (Rowley and Russell 1993), dispersal-mediated gene flow may be high along rivers where habitat is well connected. However, long sections of river that contain little habitat are strong barriers to gene flow. This is evidenced by the high genetic differentiation of the Durack and Bindoola populations which are connected by waterway (Figure 5.5). It appears most dispersal occurs along waterways, because populations of *M. c. coronatus* in adjacent catchments can be moderately to highly divergent (Table 5.2 & 5.3; Figure 5.2 & 5.5). This pattern of genetic structure is similar to that described in the Stream Hierarchy model of genetic subdivision in freshwater fishes (Meffe and Vrijenhoek 1988). The population genetic structure of purple-crowned fairy-wrens is similar to that of freshwater rainbowfish (*Melanotaenia australis*) occurring on the same waterways in the Kimberley region (Young *et. al.* 2011). However unlike many freshwater fish species (Hughes 2007), purple-crowned fairy-wrens may occasionally

disperse between catchment headwaters that are in close proximity, as evidenced by the low genetic divergence of populations on the Fitzroy and Durack (Table 5.2; Figure 5.5).

Although the Durack and Fitzroy populations may share genetic diversity due to occasional dispersal, it is likely the genetic similarity of these two populations with the Victoria River population reflects historical rather than current gene flow between these populations for three reasons. First, purple-crowned fairy-wrens on the Ord River catchment, between the Victoria River and the other central Kimberley catchments (Figure 5.1), have recently been extirpated as a result of habitat degradation (Skroblin and Legge 2010; Skroblin and Legge 2011). Second, as average natal dispersal of the purple-crowned fairy-wren is less than 3 km of river distance in quality habitat (Hall unpublished data), with very rare movements of up to 70 km of river distance (Skroblin unpublished data), it is very unlikely this species will traverse the more than 250 km of unsuitable habitat between the Kimberley and Victoria populations. Third, a lack of geographical structure in mitochondrial DNA diversity within the whole subspecies *M. c. coronatus* suggests that historical gene flow was widespread across the distribution of the subspecies (Chapter 2). The genetic similarity between the central Kimberley and Victoria populations may therefore indicate the recent isolation of these populations, combined with limited action of genetic drift within these large populations.

5.5.2. Small and isolated populations

The most genetically distinctive populations within the western subspecies were those on the Bindoola, Isdell and Drysdale catchments (Table 5.3; Figure 5.2 & 5.5). The divergence of these populations may be influenced by a combination of geographic isolation (Figure 5.1) and low population sizes (Skroblin and Legge 2010), which increases the potential for genetic drift and decreases within-population genetic diversity (Frankham 1996; Bohonak 1999; Charlesworth *et al.* 2003). Of these populations, the Isdell and Bindoola were the smallest (Skroblin and Legge 2010) and displayed decreased allelic diversity and slightly reduced levels of heterozygosity (Table 5.1). This genetic signal is consistent with these populations having been founded by a

few individuals or having experienced a bottleneck (Allendorf and Luikart 2007). However the low allelic diversity for the Bindoola catchment may be confounded by the low number of samples available (Leberg 2002). As levels of allelic diversity and heterozygosity are relatively normal for the Drysdale catchment, this population may have been isolated at a larger population size for some time. The isolation of these populations, suggests they are unlikely to be quickly re-colonized by neighbouring populations if they become extinct.

The small population of purple-crowned fairy-wrens on Bindoola Creek appears to be a remnant of a larger population of wrens that previously inhabited the Pentecost catchment (Rowley 1993; Skroblin and Legge 2010). Although this population is connected by waterway to the genetically diverse Durack population, the two appear to be functionally isolated by a barrier of approximately 140 km of river that naturally lacks suitable habitat for the species (Chapter 6). Both historical isolation, and the extensive contraction of the population following riparian degradation, have likely contributed to the genetic dissimilarity of the Bindoola population from populations on other catchments (Figure 5.2). The extremely small size and high isolation of this population place it at high risk of extinction and render re-colonisation unlikely. The Bindoola catchment accords us the best indicator of the marked effect that severe habitat degradation and contraction has on small populations of fairy-wrens because little historical information is available to infer changes in distribution on other catchments (Rowley 1993; Skroblin and Legge 2010). On the Fitzroy, where declines in the lower section of the catchment were well documented (Smith and Johnstone 1977; Rowley 1993), the remnant population appears to have been buffered against losses in genetic diversity (Table 5.1) due to its continued large size and within population connectivity.

The genetic structure found within the Victoria catchment (Figure 5.5) suggests that habitat degradation in this catchment has disrupted gene flow and produced isolated subpopulations of fairy-wrens, which may be at greater risk of decline than a large panmictic population. Individuals at the Big Horse Creek sampling site were identified as belonging to a separate genetic cluster, and may therefore be isolated from individuals that were sampled from two

other sites further upstream. Only four individuals were sampled from the Big Horse Creek site however, so caution is required in interpreting these results. Genetic divergence of the Big Horse Creek subpopulation would suggest that habitat degradation and fragmentation has been severe, and moreover that the isolated remnant populations would likely be small and at heightened risk of decline. Improved habitat connectivity along the Victoria River may be a critical conservation action to improve persistence of the subspecies throughout this catchment.

Although inbreeding may be expected to increase in small and isolated populations (Dudash and Fenster 2000; Keller and Waller 2002), no evidence of inbreeding was apparent within any population, including the Bindoola subpopulation (Table 5.1), which is the smallest subpopulation in the western subspecies (Chapter 6). This provides evidence that inbreeding avoidance may be well developed in the species, which is supported by incestuous pairings being uncommon in a study of breeding behaviour (Kingma *et al.* 2009).

5.5.3. *Consequences of future degradation and fragmentation.*

The purple-crowned fairy-wren has evolved in habitat that is naturally patchily distributed. However, the genetic structure of *M. c. coronatus* indicates that dispersal is restricted along waterways where habitat is limited and between catchments. As riparian habitat in northern Australia is experiencing ongoing degradation (National Land and Resources Audit 2002), it is likely that remnant populations of purple-crowned fairy-wrens will become increasingly genetically divergent as areas of quality habitat become ever more isolated, and decreasingly genetically diverse as populations subsequently recede in size. The effect of habitat degradation on population connectivity is already evident on the Victoria River where populations appear to be diverging genetically. Declining population size and increasing genetic differentiation of subpopulations will increase their vulnerability to extinction from interacting genetic, demographic and environmental effects (Pimm *et al.* 1988; Holsinger 2000; Ray 2001; Spielman *et al.* 2004). However, the likelihood of persistence of remnant populations may be improved by preventing further habitat destruction, in combination with, increasing the

connectivity between populations that have become isolated due to habitat degradation. Improvements to habitat connectivity may not only enhance persistence (Fahrig and Merriam 1985), but may also allow re-colonisation of small and isolated patches of suitable habitat in areas where wide-spread degradation has already lead to extinction.

CHAPTER 6

Conservation of a patchily distributed and declining species across a vast landscape: the need for a collaborative landscape-scale approach

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Format: Biological Conservation



Purple-crowned fairy-wren habitat in the Kimberley region

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6.1. Abstract

Conservation of species that are patchily distributed must consider processes that influence both the occurrence of individuals within patches, and the persistence of populations across multiple habitat patches within the landscape. Here we present a rare regional assessment of the size and distribution of a threatened species, the purple-crowned fairy-wren (*Malurus coronatus coronatus*), by predicting patch-scale occurrence across a vast landscape. We used data from aerial vegetation mapping of waterways, with on-ground bird surveys to predict the occurrence of suitable habitat for *M. c. coronatus* across 14 catchments in the Kimberley region. Suitable habitat was extremely limited (305 km) and fragmented (342 patches) along the 2700 km of waterway surveyed within catchments where the species occurs. Populations were predicted to be large on the Fitzroy, Durack and Drysdale catchments, and small on the Isdell and northern Pentecost catchments, and a total population of 2834 to 4878 individuals could be supported. The sub-populations spanned numerous patches of habitat across multiple properties of varying tenure. Therefore, a landscape-scale approach to conservation management, across multiple tenures, appears critical to safe-guard connectivity within populations. The greatest benefit may be achieved by a combination of broad-scale actions to reduce the impact of ubiquitous threatening processes, and fine-scale targeted effort in areas where populations are most vulnerable. Controlling access of stock to waterways and management of fire are most important. Such a landscape-scale approach to conservation may be of benefit to other patchily distributed species.

6.2. Introduction

Conservation of species that are distributed across small and isolated habitat patches presents specific challenges for managers. The persistence of sub-divided populations is influenced by factors operating at multiple scales (Lee *et. al.* 2002; Garden *et. al.* 2010). This includes variation in fine-scale factors such as the quality of habitat within patches (Hirzel and Le Lay

2008; Jaquierey *et al.* 2008), to landscape-scale factors such as spatial arrangement and abundance of habitat (King and With 2002), the condition of the matrix (Bender and Fahrig 2005; Fischer *et al.* 2005), and connectivity between isolated populations (Fahrig 2001; Betts *et al.* 2007; Prugh *et al.* 2008). The extent to which populations are affected by such processes is influenced by the life-history of species and the landscape context (Dupré and Ehrlén 2002).

In order to allocate conservation effort effectively at the level of sub-populations, knowledge is required of factors influencing the fine-scale distribution of populations (Araújo and Williams 2000), the spatial and temporal variation in threatening processes (Owens and Bennett 2000; Gaston *et al.* 2002), and the availability of suitable habitat at a landscape-scale (Andren 1994; Boulinier *et al.* 2001). Here we present a study which predicts patch-scale occurrence of the endangered purple-crowned fairy-wren (*Malurus coronatus coronatus*) across a vast landscape, to guide management actions for subpopulations that are distributed across widely-dispersed habitat patches.

The purple-crowned fairy-wren (*Malurus coronatus*) is a riparian habitat specialist that is restricted to small, widely-dispersed patches of lush vegetation that grow along the waterways of northern Australia. The species is pressured by the on-going degradation and loss of riparian habitat caused by grazing and trampling by introduced herbivores (Rowley 1993; DEC 2009; Skroblin and Legge 2011), weed incursion, and frequent intense fires (Woinarski 1990; Russell-Smith *et al.* 2003; Valentine *et al.* 2007). The endangered western sub-species (*Malurus coronatus coronatus*) has continued to decrease in distribution and abundance in response to these processes (Rowley 1993; van Doorn 2007; Skroblin and Legge 2010).

Until recently, the distribution of the western purple-crowned fairy-wren was poorly described due to the remoteness of the region in which it occurs; available records were mostly limited to a very small number of well visited locations (Skroblin and Legge 2010). An extensive survey for the species across the 14 catchments in the Kimberley section of its range has addressed that knowledge gap: purple-crowned fairy-wrens are distributed across a large number of small habitat patches on widely dispersed waterways within five catchments

(Skroblin and Legge 2010). Birds on each of these five catchments are genetically divergent, indicating that sub-populations are poorly connected and dispersal between catchments is restricted (Chapter 5).

Given their scattered distribution and population structure (Skroblin and Legge 2010), the species requires a region-wide assessment of the extent and location of populations to evaluate the most appropriate approach to ensure the persistence of population processes and key sub-populations. This study describes the fine-scale distribution of suitable habitat to inform such an approach within the Kimberley region of Western Australia. We develop a predictive habitat suitability model for assessing the suitability of riparian vegetation for the purple-crowned fairy-wren from aerial surveys. Using this tool, we then 1) estimate the extent of suitable habitat in the region, 2) predict the location and size of sub-populations, and 3) summarise the availability of habitat with respect to land tenure (and thus potential variation in threats). This information will allow us to identify the most effective management model for their long term conservation, which subpopulations are most at risk of further decline and whether any currently ‘unoccupied’ waterways contain sufficient habitat for purple-crowned fairy-wrens.

6.3. Methods

6.3.1. Survey design

The study was conducted in the Kimberley region of Western Australia during the dry seasons of 2007 (May-Oct), 2008 (May-Oct) and 2009 (July). We sought to map the distribution of a large number of highly dispersed habitat patches in a region with very limited road access. Ground surveys were therefore not possible. Standard remote sensing techniques were also inadequate because we needed to classify understorey vegetation beneath a canopy (Wang *et. al.* 2009; Estes *et. al.* 2010). Consequently, aerial survey using an R44 helicopter and a handheld GPS (Garmin GPSmap 60, Schaffhausen, Switzerland) was the only feasible way to map and describe the riparian vegetation.

In order to generate accurate estimates for habitat extent and population sizes, the aerial surveys were geographically extensive. They included all sections of waterways within the region where the purple-crowned fairy-wren has been recorded (Atlas of Australian Birds, September 1998–July 2007. Birds Australia, Melbourne; Rowley 1993; Skroblin & Legge 2010), and all sections of waterway where dense riparian vegetation could be identified from low resolution satellite images (Google Earth). Specifically, surveys traversed 1) all five catchments where the species currently occurs (Fitzroy, Durack, Isdell, Drysdale and Pentecost), 2) a section of the Ord catchment from which the species recently disappeared, and 3) sections of eight additional catchments (Sale-Berkelman, Forrest, Berkeley, King George, Calder, Charnley and Carson) that may contain suitable habitat, but on which purple-crowned fairy-wrens have never been recorded (Skroblin and Legge 2010). Surveys did not include the Victoria River section of the species distribution where habitat has been previously surveyed (van Doorn 2007), or rivers in the north-western Kimberley (in the Prince Regent Nature Reserve and on the Mitchell Plateau), as they have often been visited by biologists and purple-crowned fairy-wrens have never been recorded. In total, 47 sections of waterway were surveyed (Table 6.1), and the surveys traversed 37 properties of varying tenure.

6.3.2. *Vegetation mapping*

In the study region, riparian vegetation grows as narrow belts along rivers banks, thereby causing a linear arrangement of territories of the purple-crowned fairy-wren, which strictly depend on this vegetation (Rowley and Russell 1993; Kingma *et al.* 2009). Territory size is best measured as the length of waterway held by a territorial group (Rowley and Russell 1993), and the length of suitable habitat along a waterway determines the number of territories that can be supported (Rowley 1993). Based on this knowledge we used habitat patch length as our metric of habitat extent.

Table 6.1. Sections of waterways surveyed in the Kimberley region for riparian vegetation suitable for the purple-crowned fairy-wren. Latitude and Longitude is in decimal degrees.

River system	No.	Name	Survey start		Survey finish		PCFW
			Lat (° S)	Long (° E)	Lat (° S)	Long (° E)	
Fitzroy	1	Adcock River	-17.553	126.143	-17.150	125.728	y
	2	Annie Creek	-17.495	126.113	-17.534	126.110	y
	3	Bella Creek	-16.626	126.481	-16.512	126.403	y
	4	Fitzroy River (south)	-18.087	124.180	-18.193	124.491	n
	5	Fitzroy River (upper)	-17.499	126.684	-18.393	124.575	y
	6	Grey Mare Creek	-17.363	126.104	-17.368	126.094	y
	7	Hann River	-16.513	126.356	-17.435	126.301	y
	8	Little Gold River	-18.000	126.491	-18.001	126.766	y
	9	Manning Creek	-16.466	125.888	-16.851	126.059	y
	10	Margaret River	-18.555	126.632	-18.154	125.762	y
	11	O'Donnell River	-18.349	126.603	-18.249	126.823	n
	12	Roy Creek	-17.465	126.183	-17.539	126.197	y
	13	Spider Creek	-17.617	126.151	-17.634	126.177	y
	14	Throssell River	-17.368	126.094	-17.493	126.052	y
	15	Traine River	-16.919	126.546	-17.332	126.305	y
	16	Clean Skin Creek	-17.153	126.452	-17.055	126.764	n
	17	Yellow Creek	-17.079	126.404	-17.138	126.303	y
	18	Traine River Trib	-16.917	126.545	-16.759	126.505	y
Isdell	19	Bell Creek North	-16.875	125.158	-17.061	125.254	y
	20	Isdell River East	-16.720	125.933	-16.571	125.807	y
	21	Isdell River West	-17.017	125.404	-16.433	124.836	y
Drysdale	22	Banjo Creek	-15.263	126.911	-15.409	127.172	y
	23	Drysdale River	-15.984	125.984	-14.247	126.937	y
	24	Gibb River	-15.620	126.625	-16.252	126.366	y
Durack	25	Blackfellow Creek	-16.300	126.978	-16.756	126.756	y
	26	Chapman River	-16.701	126.545	-16.044	127.201	y
	27	Durack River	-15.598	127.832	-17.119	127.138	y
	28	Ellenbrae Creek	-15.845	126.753	-15.899	127.220	n
	29	Leopold River	-17.766	126.646	-18.304	126.647	y
	30	Wood River	-16.619	127.101	-17.053	126.835	y
Pentecost - north	31	Bindoola Creek	-15.703	127.853	-15.784	127.723	y
	32	Pentecost River	-15.972	127.928	-15.703	127.853	n
Forrest	33	Forrest River	-15.201	127.810	-15.226	127.297	n
Berkley	34	Berkley River	-15.177	127.247	-14.835	127.649	n
King George	35	King George River	-14.544	127.315	-14.068	127.311	n
Sale	36	Sale River	-16.067	124.822	-15.927	125.117	n
Calder	37	Calder River	-16.063	125.211	-16.369	124.953	n
Charnley	38	Charnley River	-16.259	125.363	-16.303	125.894	n
Ord	39	Bow River	-16.827	128.364	-16.696	128.644	n
	40	Negri	-17.090	128.889	-17.073	129.000	n
	41	Ord River	-16.617	128.640	-17.213	128.884	n
	42	Turkey Creek	-17.016	128.226	-16.827	128.364	n
Pentecost - south	43	Chamberlain River	-17.236	127.063	-15.972	127.928	n
	44	Chamberlain Trib	-17.280	127.242	-17.324	127.261	n
Carson	45	Carson River	-14.425	126.639	-15.220	126.514	n
	46	King Edward River	-14.967	126.128	-14.425	126.639	n
	47	Morgan River	-14.753	126.777	-14.974	126.314	n

6.3.3. Vegetation attributes

Previous studies have identified the key vegetation characteristics that are a pre-requisite for occupancy by purple-crowned fairy-wrens. These are a dense mid-storey (of *Pandanus*, river grass and/or freshwater mangrove), which is important for nesting and shelter, and a high canopy which acts as a temporary refuge during the flooding events that often occur during the summer monsoons (Rowley 1993; van Doorn and Low Choy 2009; Skroblin and Legge 2011). We therefore only mapped patches of vegetation that contained both canopy and understorey structure.

We selected a simple set of mid-storey and canopy attributes that could be reliably scored from aerial surveys. These were: the percentage of bank covered with either: 1) *Pandanus*, 2) tall river grasses (such as *Chionachne cyanthopoda*), and 3) shrubs; plus 4) the canopy cover across a patch; and 5) the height of canopy in relation to flood height. To enable surveys to be conducted rapidly, we recorded predictors as categorical values (Table 6.2). The location and extent of patches were recorded using a hand-held GPS, and a geographic information system (ArcGIS V9.2, ESRI) was used to determine the length of habitat patches, the number of patches, the total extent of riparian vegetation for each catchment, and to produce maps of vegetation configuration (Guisan and Zimmermann 2000; Gibson *et al.* 2004).

Table 6.2. Vegetation attributes of patches recorded during aerial vegetation mapping

Patch attribute	Median (range)	Description
Canopy height	5 (1-5)	1) Below flood level, 3) above flood level but <10m, 5) above flood level and >10m
Canopy cover	5 (1-5)	Continuity of over-storey: 1) <25%, 3) 25-75%, 5) >75%
Shrub cover	5 (1-5)	Mid-storey other than <i>Pandanus</i> and river grass: 1) <5%, 3) 5 – 50%, 5) >50% bank covered
<i>Pandanus</i> cover	2 (1-5)	Bank covered with <i>Pandanus</i> : 1) Absent, 2) <25%, 3) 25-50%, 4) 50-75%, 5) >75%
River grass cover	1 (1-5)	River grass cover: 1) none, 3) <50% river grass cover, 5) >50%

6.3.4. Bird surveys

To develop the predictive habitat suitability model based on aerial vegetation assessments, we conducted on-ground surveys for the presence of purple-crowned fairy-wrens within vegetation patches. Surveys were conducted at a subset (113) of the aerially mapped patches on five catchments where the species currently occurs (Skroblin and Legge 2010). We did not include sites from outside the current distribution of the species, as absence from these areas may be influenced by limits to colonization rather than the suitability of habitat (Theodorou and Couvet 2009).

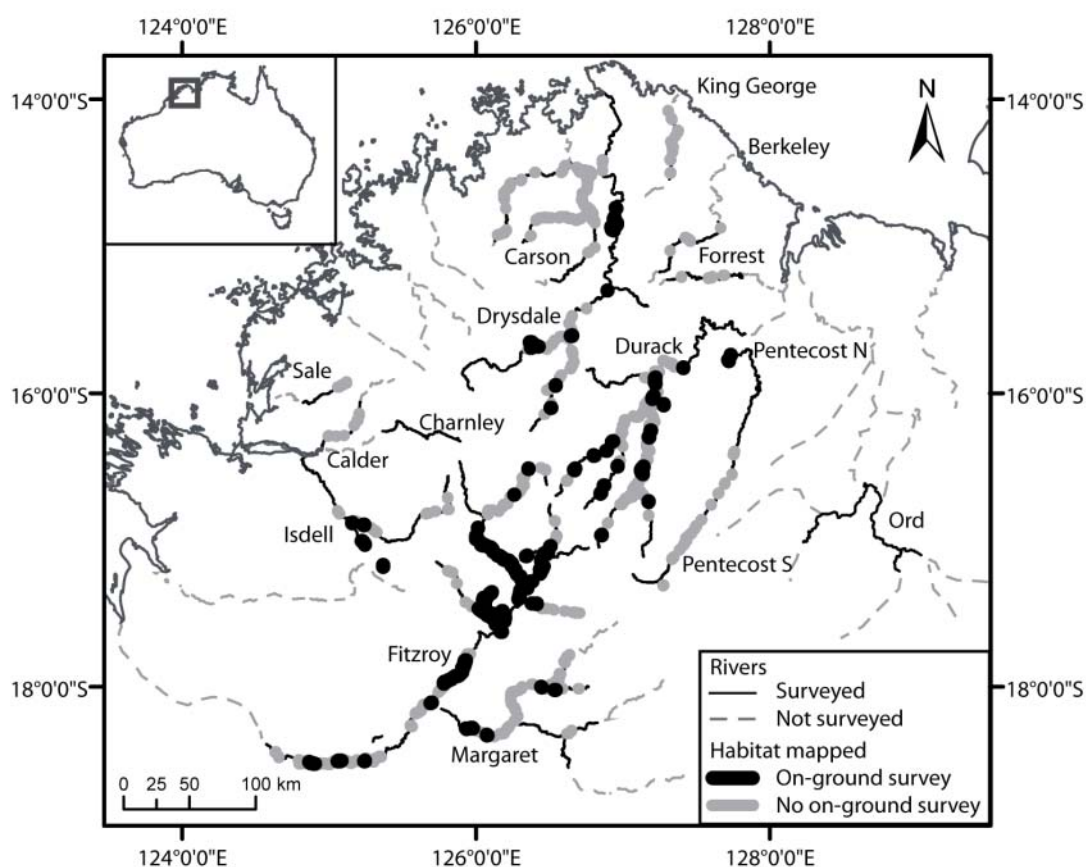


Figure 6.1. Riparian vegetation mapped during helicopter surveys of waterways in the Kimberley region of Western Australia. All patches that were mapped contained both canopy and mid-storey structure. Rivers that were surveyed are described in Table 6.1. On ground bird surveys were conducted in the patches that are indicated in black (N=113). Patches surveyed for birds were along waterways where purple-crowned fairy-wrens occur and were used to generate the predictive model of habitat suitability

We surveyed for purple-crowned fairy-wrens in a minimum of three patches of vegetation on each section of river that was mapped by air (Table 6.1), giving preference to patches that were long enough to contain territories ($> 300\text{m}$). Either the entire patch (if $< 1\text{km}$) or a minimum of 1km of riparian vegetation was surveyed in each instance. In total, bird surveys were conducted within 79 patches on the Fitzroy, five patches on the Isdell, 12 patches on Drysdale, three patches on the northern Pentecost, and 19 patches on the Durack catchments (Figure 6.1). Surveys were conducted following the high detection method of Skroblin and Legge (2010). Briefly, we walked within or along the edge of riparian vegetation and broadcast *M. c. coronatus* territorial calls to assist in detection of this highly territorial species (Hall and Peters 2008).

6.3.5. Statistical data analysis

Using the data from the patches that were surveyed on-ground for the presence of purple-crowned fairy-wrens, we developed a logistic model to predict the suitability of mapped riparian vegetation. When developing this model, river grass cover was not included as an explanatory variable because it was only encountered at one of the patches that was surveyed on-ground. Prior to modelling, correlations between vegetation attributes were computed and examined for multicollinearity. Analyses were conducted in GenStat 11.1 (VSN International).

We used generalized linear modelling (GLM) with binomial error distribution and a logit link function (McCulloch *et. al.* 2008) to evaluate the fit of twelve combinations of the patch vegetation attributes in explaining occurrence of the purple-crowned fairy-wren. These combinations all contained a mid-storey parameter and a canopy parameter, because both structures are known to be integral components of suitable habitat. Our modelling approach used the multi-modal inference framework (Burnham and Anderson 2002), and employed the Akaike Information Criterion adjusted for small sample size (AIC_c). Firstly, Akaike weights (Akaike 1974) were calculated for each candidate model relative to the likelihood of a model. An Akaike weight (ω_i), is the weight of evidence in favour of a candidate model (i), being the

best approximating model in the set of models available. We then obtained a 90% confidence set of plausible candidate models by summing Akaike weights of models (from smallest to largest) until the sum was ≥ 0.9 . A weighted model-averaging approach was then employed to calculate the summed Akaike weights for each predictor variable and also the averaged partial regression coefficients from the models within the 90% confidence set (Burnham and Anderson 2002). For a secondary measure of model rankings, Adjusted R^2 was also calculated (Mac Nally 2000). Catchment was initially included as a random term to account for spatial structure of sampling but did not improve the fit of models to the data and was subsequently excluded.

The final model, containing the model-averaged partial regression coefficients, was fitted to the vegetation attributes of every patch mapped during aerial surveys. We performed inverse logistic transformation of the linear predictor to calculate habitat suitability as values between zero and one (Guisan and Zimmermann 2000). To delineate riparian vegetation into potentially *suitable* and *unfavourable* habitat, we identified the minimum predicted habitat suitability score at which purple-crowned fairy-wrens were found to be present during bird surveys. This threshold was used to identify which patches mapped during aerial surveys contained *suitable* habitat. Only patches that were classified as potentially *suitable* were included in summaries of habitat distribution across land tenure types and in calculations of population estimates, below.

6.3.6. *Distribution of suitable habitat across land tenure types*

We summarized the availability of habitat with respect to land tenure by assigning habitat to categories based on five land tenures: 1) pastoral (pastoral land, including indigenous managed); 2) vacant Crown Land; 3) conservation (National Parks and Conservation Parks); 4) private conservation (Australian Wildlife Conservancy land with a pastoral history that is now managed for conservation); and 5) indigenous (indigenous land reserves, excluding indigenous pastoral). Where habitat patches were on waterways separating lands of differing tenure, the tenure of highest *theoretical* impact was assigned, i.e. habitat between conservation and pastoral land was assigned as pastoral.

6.3.7. Population estimates

We estimated the number of territories and absolute population size that each catchment could potentially support, by combining information on demographic data (Rowley and Russell 1993; Skroblin and Legge 2010) with our map of suitable habitat. Because estimation of population size is complicated by variation in the number of birds within a territorial group and variation in the length of territories, we estimated upper and lower population estimates for each catchment to account for this variation. We calculated: 1) upper and lower 95% confidence intervals for the mean number of birds per territory (2.8 and 3.2) from group size data for 167 purple-crowned fairy-wren territories surveyed in the Kimberley region (Skroblin and Legge 2010), 2) upper and lower estimates of mean number of territories per kilometre (3.34 and 5) using Rowley and Russell's (1993) estimate of territories being between 200 to 300m in length in the Kimberley region, and 3) the resulting upper and lower mean number of birds per kilometre of habitat (9.3 and 16). Absolute population size (N) was calculated as the product of the mean number of birds per kilometre of suitable habitat and the length of suitable habitat:

$$N = \text{average birds per km} \times \text{length suitable habitat}$$

6.4. Results

6.4.1. Survey findings

We surveyed approximately 4000 km of waterway within the Kimberley region, of which 490 km contained vegetation that included a canopy and mid-storey structure (Table 6.3). The highest extents of riparian vegetation were documented on rivers where the species occurs: the Fitzroy (241 km), Durack (98 km), and Drysdale (47 km) Rivers. Relatively little riparian vegetation was documented on catchments where the species does not occur, with the exception of the Carson catchment (61 km) (Table 6.3).

Table 6.3. Summary of the extent of riparian vegetation mapped during aerial surveys of 14 catchments within the Kimberley region. Riparian vegetation that was mapped contained both canopy and mid-storey structure.

Catchment	PCFW	Survey distance (km)	Vegetation (km)	Number of patches
Fitzroy	Y	1316	241	207
Isdell	Y	236	12	23
Drysdale	Y	566	47	60
Durack	Y	641	98	113
Pentecost - north	Y	25	3	5
Subtotal		2784	401	408
Ord	N	367	0	0
Forrest	N	88	2	5
Berkeley	N	87	1.6	5
King George	N	63	7.2	14
Sale	N	41	2.6	4
Calder	N	141	2.7	10
Charnley	N	78	0	0
Pentecost - south	N	174	11	21
Carson	N	252	61	66
Subtotal		1213	88	125
Total		3997	490	533

6.4.2. Model of habitat suitability

Correlations between vegetation attributes were all less than $r = 0.25$ (Table 6.4) and thus multicollinearity between variables was low. The best approximating multivariate model of habitat suitability contained the predictors of shrub cover, *Pandanus* cover and canopy height (GLM, $df = 3, 112$, deviance ratio = 5.11, $P = 0.002$). This model had the lowest AIC_c value (Table 6.5); however the Akaike weight of 0.28 for this model suggests substantial model selection uncertainty. Moreover, support for the second model was also strong with a 0.047 difference in Akaike weights between the two (Table 6.5). Eight models were included in the 90% confidence set of plausible candidate models (Table 6.5), so uncertainty of model 1 being the best model was considerable. Hence it was appropriate to undertake model averaging within the 90% confidence set of models to develop a predictive model of habitat suitability (Table 6.6).

Table 6.4. Correlations between patch attributes for catchments within the current range of the purple-crowned fairy-wren. Significance levels ($P < 0.05 = *$). $N = 113$.

	Canopy cover	Canopy height	Shrub cover
Canopy height	0.151		
Shrub cover	0.118	0.229*	
<i>Pandanus</i> cover	0.117	0.192*	0.077

Table 6.5. Results of model selection using a multi-model inference framework for habitat suitability of riparian vegetation patches for the purple-crowned fairy-wren. All evaluated models are shown, those above the line were included in the 90% confidence set of models.

The table shows the number of terms in the model (K), Akaike Information Criteria adjusted for small sample size (AIC_c), AIC_c differences (Δ_i), the likelihood of model i given the data ($L(g_i|x)$), Akaike weights (ω_i), and Adjusted R-square ($AdjR^2$). Explanatory variables: S = shrubs; P = *Pandanus*; CH = canopy height; CC = canopy cover.

Rank	Explanatory variables	K	AIC_c	Δ_i	$L(g_i x)$	ω_i	$AdjR^2$
1	S + P + CH	4	116.62	0.00	1	0.280	10.44
2	S + P	3	116.99	0.37	0.83	0.233	9.31
3	S + P + CC + CH	5	118.56	1.94	0.38	0.106	9.66
4	S + CH	3	118.58	1.96	0.37	0.105	8.00
5	S + P + CC	4	118.97	2.35	0.31	0.087	8.49
6	P + CC	3	120.01	3.39	0.18	0.051	6.83
7	S	2	120.55	3.93	0.14	0.039	5.6
8	S + CC + CH	4	120.57	3.95	0.14	0.039	7.16
9	P + CC + CH	4	121.99	5.37	0.07	0.019	5.99
10	P	2	122.12	5.5	0.06	0.018	4.32
11	S + CC	3	122.52	5.9	0.05	0.015	4.76
12	P + CC	3	124.10	7.48	0.02	0.007	3.47

Table 6.6. Model averaged coefficients, standard errors and weighting for each variable included in the 90% confidence set of models.

Explanatory terms	Coefficient	SE	Weight
Constant	-11.561	17.95	
Canopy cover	-0.014	0.08	0.246
Canopy height	2.068	3.51	0.619
Shrub cover	0.381	0.22	0.945
<i>Pandanus</i> cover	0.442	0.15	0.805

The final model, which predicts habitat suitability scores between zero and one, contained the model-averaged partial regression coefficients (Table 6.6):

$$1 - \left(\frac{1}{1 + e^Y} \right) = -11.561 - 0.014(\text{canopy cover}) + 2.068(\text{canopy height}) \\ + 0.381(\text{shrub cover}) + 0.442(\text{Pandanus density})$$

Our modelling approach indicated that a dense mid-storey of shrubs and *Pandanus*, and high canopy and continuity of canopy cover, when measured during helicopter survey, were appropriate predictors of purple-crowned fairy-wren occurrence (assessed in ground surveys) in the Kimberley region (Table 6.5). The most highly weighted and thus important predictors of occurrence were shrub cover, *Pandanus* cover and canopy height, while canopy cover was less important (Table 6.6). The slightly negative coefficient of canopy cover (Table 6.6) may indicate that trees that are tall enough to provide refuge from flooding grow at low density along river verges. As 98% of fairy-wrens were detected in patches with HS > 0.5, we identified this as a threshold to purple-crowned fairy-wren occurrence. Thus we consider only patches with HS > 0.5 as *suitable* habitat, and all patches < 0.5 as being *unfavourable* for the species.

6.4.3. Distribution of suitable habitat

Catchments where purple-crowned fairy-wrens occur

Of the catchments where the purple-crowned fairy-wren occurs, the Fitzroy, Durack and Drysdale contained large extents of suitable habitat (HS > 0.5), whereas the Isdell and northern Pentecost catchments contained a limited amount of suitable habitat (Figures 2 & 3). The vast majority of suitable habitat (77%) was located on pastoral lands, with only 17% located on conservation lands (private and government), and a small extent on vacant Crown Land (6%). No indigenous lands were present within the watersheds containing populations of purple-crowned fairy-wrens (Figure 6.3). Most habitat occurring on conservation land was located in three reserves: Mornington Wildlife Sanctuary (private conservation; Fitzroy catchment),

Drysdale National Park (conservation; Drysdale catchment), and King Leopold Conservation Park (conservation; Isdell catchment).

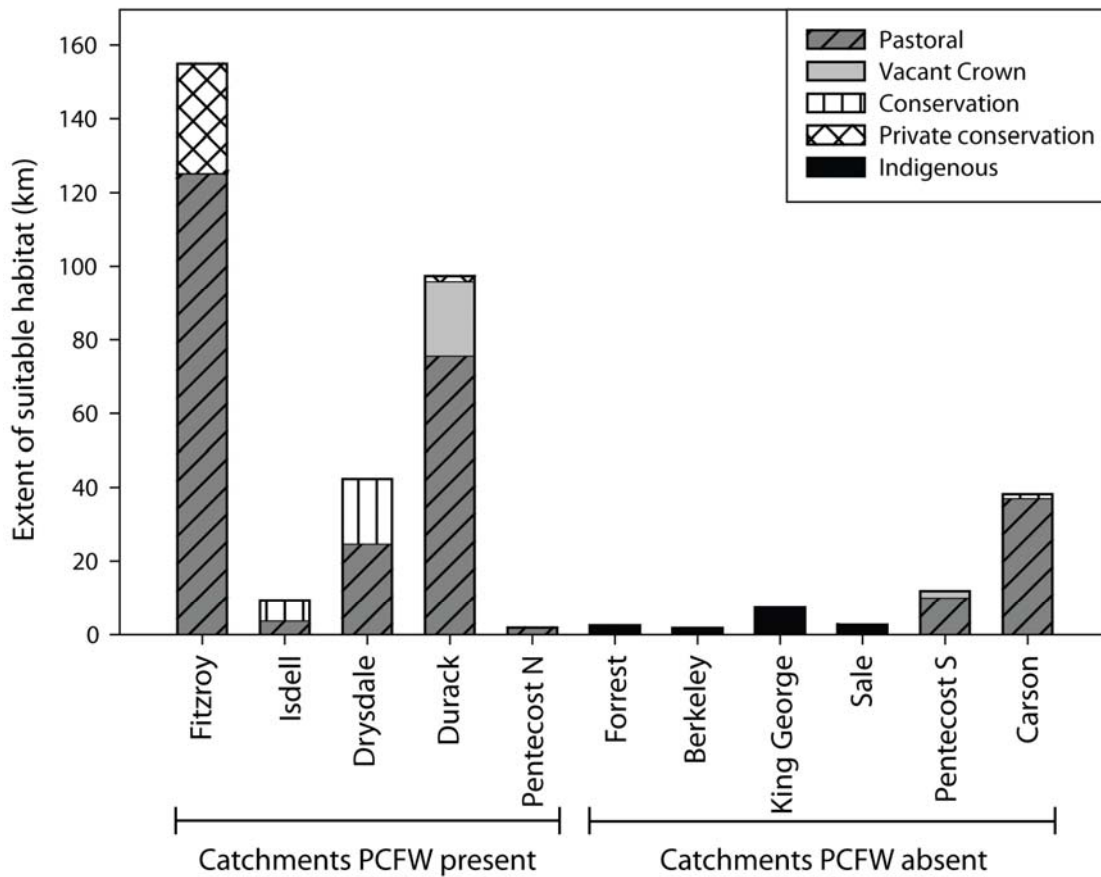


Figure 6.2. The predicted extent of suitable habitat ($HS > 0.5$) for the purple-crowned fairy-wren across catchments in the Kimberley Region with respect to land tenure. Catchments are designated PCFW present if they belong to the current distribution of the purple-crowned fairy-wren, and PCFW absent if the species does not occur on them. The Ord and Charnley Rivers are not depicted as no suitable habitat was detected on these rivers.

In the Fitzroy catchment, 125 km (81%) of suitable habitat was found on pastoral land and 29 km (19%) on conservation land (mostly on Mornington Wildlife Sanctuary, with a small extent in Geike Gorge National Park) (Figure 6.2). The majority of suitable habitat was located in the mid to upper sections of the catchment, on the Hann, Fitzroy, Adcock, and Throssell Rivers, as well as Annie Creek. Areas to the south of Dimond Gorge contained habitat that was generally

unfavourable, with the exception of a few stretches of high quality habitat on the Margaret and Leopold Rivers (Figure 6.2).

The Durack catchment contained the second highest cumulative length of suitable habitat (Figure 6.3). The majority of habitat (76 km; 77%) was located on Karunjie (indigenous pastoral lease) and Wood River (vacant Crown Land; 21%), with a small extent (1.4 km) on Marion Downs Wildlife Sanctuary (private conservation). The third highest length of suitable habitat was identified on the Drysdale catchment (Figure 6.3), where most habitat occurred on pastoral land (58%), with the remainder (17.5 km) in Drysdale National Park (Figure 6.2).

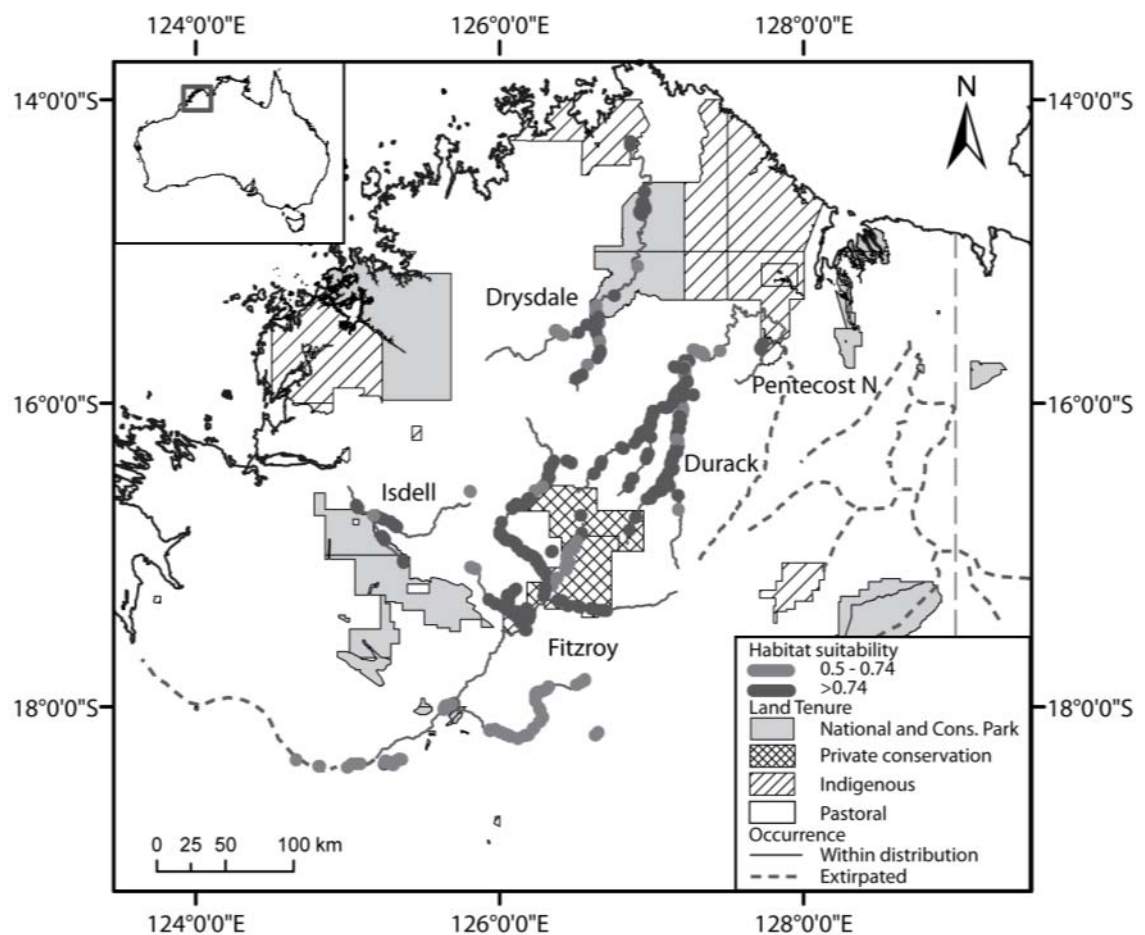


Figure 6.3. The predicted location of suitable riparian vegetation for the purple-crowned fairy-wren within the Kimberley region. Only rivers where the species now occurs or previously occurred but has since disappeared are indicated.

The Isdell and northern sections of the Pentecost catchment contained comparably little habitat (Figure 6.2). Suitable habitat within the Isdell catchment was located on Bell Creek in the King Leopold Conservation Park (5.4 km; 58%) and on a section of the Isdell River which forms a boundary between the eastern edge of the Conservation Park and pastoral land (3.8 km; 42%). Within the area that was mapped on the northern Pentecost catchment, the population of purple-crowned fairy-wrens appears to be limited to five patches of suitable habitat (totalling 3 km), all on pastoral land (Figure 6.2 & 6.3).

Catchments where purple-crowned fairy-wrens do not occur

Suitable habitat was generally limited on catchments where purple-crowned fairy-wrens do not occur, with the exception of the Carson in the northern Kimberley (Figure 6.2 & 6.3). Less than 5 km of suitable habitat was identified on each of the Forrest, Berkeley, Sale, and Calder, and slightly more on the King George (7.3 km) and southern Pentecost (11.8 km) catchments. No suitable habitat was located on the sections of the Ord catchment or Charnley River that were surveyed (Table 6.3).

6.4.4. Population estimates

We estimate that between 1013 and 1524 territories of purple-crowned fairy-wrens equating to 2834 to 4878 individuals may be supported by the extent of suitable habitat available to this species in the Kimberley region (Table 6.7). Large populations were located on the Fitzroy, Durack and Drysdale, and two smaller populations were located on the Isdell and northern Pentecost catchments (Table 6.7). Many of the catchments where the species does not occur contain habitat that could only support very small, and perhaps unsustainable, populations. We estimate that only the Carson could potentially support a large population (355 – 600; Table 6.7).

Table 6.7. Estimates of the extent of suitable habitat and the resulting *theoretical* number of purple-crowned fairy-wrens and their territories that could occur on 14 catchments within the Kimberley region.

Population size estimates were based on the predicted extent of suitable habitat within each catchment and information on group size and territory length. Lower (Length x 9.3); upper (Length x 16). Present = status of purple-crowned fairy-wren distribution within the catchment; suitable habitat = $HS > 0.5$; N = absolute population size.

Catchment	Suitable habitat		Territories		N	
	patches	extent (km)	lower	upper	lower	upper
<i><u>PCFW present</u></i>						
Fitzroy	155	154	513	771	1434	2467
Isdell	21	9	30	46	85	147
Drysdale	50	42	140	212	393	677
Durack	111	97	324	486	905	1557
Pentecost N	5	3	6	9	17	30
Sub total	342	305	1013	1524	2834	4878
<i><u>PCFW absent</u></i>						
Ord	0	0	0	0	0	0
Forrest	5	2	8	12	22	38
Berkeley	5	2	6	9	16	27
King George	14	7	24	37	67	115
Sale	4	3	9	14	25	43
Calder	10	3	9	14	26	45
Charnley	0	0	0	0	0	0
Pentecost S	21	12	39	59	109	188
Carson	53	38	126	191	355	611
Total	454	372	1234	1860	3455	5947

6.5. Discussion

Our survey shows that habitat suitable for the purple-crowned fairy-wren was limited in extent and had an extremely patchy distribution along waterways within the Kimberley region. The five sub-populations of purple-crowned fairy-wrens occurring in the Kimberley region were restricted to 305 km of potentially suitable habitat that was dispersed as 342 patches along 2700 km of waterway (11% of the waterways; Table 6.7). Sub-populations spanned multiple patches of habitat on each of the five catchments where the species occurs, and the viability of each of

the five sub-populations was likely to vary depending on population size and connectivity (Pimm *et al.* 1988; Holsinger 2000). Populations most at risk of extinction were likely the extremely small Isdell and northern Pentecost sub-populations, while the larger Fitzroy, Durack and Drysdale sub-populations were more secure.

6.5.1. Determinants of distribution

The distribution of the purple-crowned fairy-wren in the Kimberley region appears to be influenced by the extent of suitable habitat as well as barriers to dispersal. The species occurred as three large populations (Fitzroy, Durack and Drysdale) and two smaller populations (Isdell and northern Pentecost) on catchments in the central Kimberley. Habitat was insufficient to support populations of fairy-wrens on the other catchments that were surveyed, except potentially for the Carson and the lower section of the Pentecost catchments (Figure 6.2). As most purple-crowned fairy-wren dispersal occurs along waterways (Chapter 5), colonization of the Carson catchment maybe impeded by the Carson Escarpment and the Ashton Range, which separate the Carson from the nearest population on the Drysdale river by an overland distance of greater than 30 km. Similarly, colonization of the southern section of the Pentecost catchment may be prevented by the 100 km long Chamberlain Gorge which is naturally devoid of riparian vegetation. Further research is required to investigate whether other factors, such as patterns of habitat fragmentation (Prugh *et al.* 2008; Ritchie *et. al.* 2009; Wilson *et al.* 2009), may also limit occurrence of the species in these areas.

6.5.2. Conservation approach – regional-scale

Habitat for the purple-crowned fairy-wren occurs mainly on pastoral land and was widely dispersed along waterways in the Kimberley region. A conventional system of reserves will therefore neither capture a large enough sub-population of wrens to ensure their persistence, nor safeguard connectivity between sub-populations and thus the maintenance of key population processes such as dispersal (Soulé *et al.* 2006). Moreover, the key threats to purple-crowned fairy-wrens and other biodiversity in the Kimberley (changes in fire patterns, introduced

herbivores, feral cats, invasive weeds) currently affect all tenures in the region more or less indiscriminately, so that tenure designation as conservation land does not confer protection (Carwardine *et. al.* 2011).

Conservation of the purple-crowned fairy-wren requires improved land management at a regional-scale to protect riparian habitat across all tenures. It is likely that the persistence of many other species in northern Australia, including those with more cryptic population structure, will require landscape-scale conservation approaches (Woinarski *et. al.* 1992; Dickman *et. al.* 1995). This will entail cooperation among multiple land holders to collaborate on stewardship for multiple goals, including production, ecological sustainability and biodiversity conservation (Hobbs and Saunders 1991; Morton *et. al.* 1995). The positive outcomes of such an approach has already been demonstrated in the Kimberley region by two programs in particular. The regional donkey control program managed by the Department of Food and Agriculture Western Australia has reduced the standing herd of donkeys in the region from around 600,000 to less than 20,000 (M. Everrit, pers.comm.). Similarly, EcoFire (Legge *et al.* 2011), is a partnership between landholders, private conservation and government agencies to manage fire cooperatively over 4 million hectares of the central and north Kimberley. This project has delivered a prescribed burning program that has reduced the incidence of extensive, intense fires. An associated monitoring program for selected biological indicators has demonstrated, amongst other metrics, that the complete exclusion of fire at a focal monitoring site coincided with the expansion and thickening of (fire-sensitive) riparian vegetation and an increase in the population size of purple-crowned fairy-wrens (Legge *et al.* 2011).

6.5.3. Management directives

Landscape scale

The main threats to the riparian habitat of purple-crowned fairy-wrens (introduced herbivores, frequent intense fire, weed invasion) (Rowley 1993; van Doorn 2007; Skroblin and Legge 2011), are ubiquitous across the savannahs and tenures of northern Australia (Russell-

Smith *et al.* 2003; Woinarski and Fisher 2003; Yates *et al.* 2008). Thus, management goals for improving the persistence of purple-crowned fairy-wrens and other riparian specialists are similar across land tenures. Stock access to riparian areas needs to be controlled and the incidence of intense fires needs to be reduced. These management initiatives can benefit pastoral productivity as well as biodiversity. Provisioning alternative water sources away from waterways distributes grazing more uniformly and increases pasture utilisation (Hunt *et al.* 2007) while concurrently reducing the impact of grazing and trampling on riparian vegetation structure (Jansen and Robertson 2001; Krueper *et al.* 2003; Scott *et al.* 2003), channel morphology and water quality (Belsky *et al.* 1999).

Subpopulation scale

While conservation management of the purple-crowned fairy-wren is best undertaken at a landscape scale, conservation outcomes can be improved by directing specific actions at the sub-population scale. The most urgent conservation attention may be required by the small and isolated northern Pentecost and Isdell sub-populations. Both these sub-population are genetically divergent and functionally isolated from other sub-populations (Chapter 5), and therefore at heightened risk of extinction due to their size (Pimm *et al.* 1988).

The remnant habitat on the northern Pentecost catchment may support only 30 purple-crowned fairy-wrens (Table 6.7); a population size that is unlikely to be viable. Although the habitat on the Isdell may support a population that is several times larger than that on the Pentecost (Table 6.7), it was also largely restricted to one short section of waterway and thus at high risk of total degradation through single fire or flood events (Holsinger 2000). The northern Pentecost population occurs on pastoral land and may be best protected by fencing to exclude grazing and fine-scale managed burning around habitat patches. The section of the Isdell population that occurs within King Leopold Conservation Park and may be best protected by heavily reducing the numbers of feral cattle and careful, fine-scale fire management to limit the risk of extensive, intense fires affecting the riparian vegetation. The outcome of these fine-scale

conservation actions would be enhanced by undertaking detailed on-ground surveys to assess the location of territories, the quality of habitat and fine-scale variation in threatening processes.

Although the other three populations on the Fitzroy, Durack and Drysdale are larger and thus at lower risk of immediate extinction, they are nevertheless threatened by continuing habitat degradation. These populations occur across many habitat patches on multiple properties and will thus benefit most from landscape-scale approaches to reducing threatening processes. Controlling access of stock to waterways and landscape management of fire should allow any degraded riparian habitat on these catchments to regenerate (Nelson *et al.* 2011), and will help maintain the patches of high quality habitat that occur there. Securing the high density populations in the northern Fitzroy (on the Adcock, Hann, Throssell, Annie, and tributaries) may be of higher benefit than investment in populations in the southern part of the catchment where habitat was more highly fragmented (Figure 6.3) and degraded (Skroblin and Legge 2011), and populations have already undergone significant decline.

6.6. Conclusion

This study presents a rare regional assessment of the size and distribution of a threatened species. It clearly indicates that landscape-scale conservation effort, across multiple tenures, is critical to preserving the widely-dispersed and patchily distributed purple-crowned fairy-wren within the Kimberley region. The greatest benefit may be achieved by a combination of broad-scale actions to reduce the impact of threatening processes across sub-populations, and fine-scale targeted effort in areas where populations are most vulnerable. To be successful, such off-reserve approaches would require collaboration among multiple land holders with foreseeable benefits to both biodiversity and pastoral production. Such a landscape-wide collaborative approach to conservation, may be vital for the protection of other species that are patchily-distributed (both naturally and anthropogenically) or have highly mobile populations.

CHAPTER 7

Summary and future research directions



The road ahead; Mornington Wildlife Sanctuary

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7.1. Conclusion

This thesis provides new information on the factors that influence the persistence of the purple-crowned fairy-wren and other species that inhabit riparian areas or habitats that are patchily distributed. In this final chapter I summarize the findings of this thesis, outline key management actions and briefly suggest additional research to further enhance our ability to conserve this species.

The first step in this research was to affirm the evolutionary and demographic distinctiveness of *M. c. coronatus* from the eastern subspecies of purple-crowned fairy-wren (Chapter 2). I used mitochondrial DNA to confirm that the subspecies are evolutionarily distinct lineages that can therefore be considered as separate management units for conservation. This information validated the approach taken in subsequent chapters, which focus on the conservation biology of *M. c. coronatus* in isolation from the eastern subspecies *M. c. macgillivrayi*.

Substantial adjustments to the known distribution of *M. c. coronatus* were made following extensive surveys to improve fine-scale knowledge of the species occurrence (Chapter 3). This thesis describes several previously unreported populations, and demonstrates that *M. c. coronatus* was either extremely limited in number or absent from some rivers that were previously included in the ‘known’ distribution. A comparison of the updated distribution with historical records confirmed that the species had disappeared from several watercourses and has continued to decline in distribution.

The distribution of populations of *M. c. coronatus* was constrained by the quality and extent of riparian vegetation along waterways (Chapter 4). The species was found in areas that contained a dense canopy of emergent trees, in addition to a well-developed mid-storey that was comprised of shrubs (i.e. *Pandanus* or *Barringtonia*) or river grass (*Chionachne*). Broad-scale degradation of the understorey due to grazing and fire has caused the disappearance of *M. c. coronatus* from sections of its former range. Without intervention to control access of stock to riparian areas and to limit the impact of intense fires on riparian vegetation, riparian habitat in the Kimberley region will continue to be degraded.

Analysis of population genetics revealed that *M. c. coronatus* occurs as six genetically divergent sub-populations that correspond to catchment boundaries or expansive gaps in habitat along waterways (Chapter 5). These populations differed in size and extent of isolation: three large populations were similar genetically and three smaller populations were highly distinctive due to their isolation. The pattern of genetic divergence between and within populations indicates that degradation of riparian areas has disrupted connectivity between remnant populations. Persistence of *M. c. coronatus* may therefore be improved by strategies that maintain connectivity and reduce continuing riparian degradation.

Extensive aerial vegetation mapping, in combination with habitat modelling, indicated that habitat for the purple-crowned fairy-wren is extremely limited and widely-dispersed along waterways (Chapter 6). Due to this spatial arrangement, it is unlikely that a conventional system of reserves would capture large enough populations to ensure their persistence or maintain connectivity within populations. The best approach to conservation of the species may be management across multiple properties and tenures that combines broad-scale actions to reduce the impact of ubiquitous threatening processes (introduced herbivores, intense fires, weed incursion), with fine-scale targeted effort in areas where populations are most vulnerable. A similar landscape-scale approach to conservation may be beneficial to other patchily distributed species (whether naturally or anthropogenically so).

A region-wide management initiative is needed to conserve *M. c. coronatus*. This initiative must include actions that occur at the landscape, catchment and patch scale. At the landscape scale, controlling access of stock to riparian areas and limiting the frequency of intensive fires will help maintain patches of high quality habitat and allow degraded areas to regenerate. Catchment scale management is vital to ensure connectivity within populations that are widely dispersed across many patches of habitat. Fine-scale actions are required to safeguard the persistence of small and isolated sub-populations and may include fencing of areas that have high conservation value, and careful localized back-burning around important patches of habitat.

The outcome of management to conserve the purple-crowned fairy-wren could be enhanced by further research that examines what thresholds to persistence are experienced by the species within fragmented landscapes. An understanding of the range of distances and conditions across which individuals are capable of dispersing will help highlight areas where connectivity between habitat may be depleted, and conservation effort is thus required. The population genetic structure of the species suggests it generally disperses along waterways. This could be explicitly tested using a combination of fine-scale genetic data and observation of dispersal behaviour. It would furthermore be interesting to examine whether knowledge of the adaptations that enable species, such as the purple-crowned fairy-wren, to persist in extremely patchily distributed habitat could be applied to predict the impact anthropogenic fragmentation may have on species with differing life histories.

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9. APPENDIX

Australian Freshwater Crocodile (*Crocodylus johnstoni*) Attacks on Humans

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Australian freshwater crocodile in the Ord River

©Anja Skroblin

A.1. Introduction

Both *Crocodylus johnstoni* (Australian Freshwater Crocodile) and *C. porosus* (Australian Saltwater or Estuarine Crocodile) occur in northern Australia. *Crocodylus porosus* is accepted as being dangerous, known to attack humans and responsible for at least 25 fatalities in Australia between 1971 and 2009 (Caldicott *et al.* 2005; C. Manolis, pers. comm.). *Crocodylus johnstoni*, on the other hand, is widely considered harmless to humans (e.g., Crocodile Specialist Group 2008; Webb and Manolis 2007). There are no recorded human fatalities from *C. johnstoni* (C. Manolis, pers. comm.) and locals frequently swim with this species, believing that it does not bite people (pers. obs.). Although it is acknowledged that *C. johnstoni* is capable of inflicting injury, both local people and experts are reluctant to believe they attack humans (Anonymous 2006; Caldicott *et al.* 2005; Crocodile Specialist Group 2008).

In September 2008, two *Crocodylus johnstoni* attacked one of the authors (KNH) in the Throssell River of the Kimberley Region of Western Australia in the presence of the second author (AS). This experience provides evidence contrary to the prevailing opinion that this species is harmless to humans. We have found additional accounts of *C. johnstoni* attacks on humans in northern Australia, but the difficulty we had in acquiring this information suggests that the widespread belief that *C. johnstoni* is harmless may in part be perpetuated by a lack of reporting, reluctance to lend credence to such accounts, and consequently a lack of media attention. These factors impede a full understanding of this species' behavior and jeopardize public safety. We discuss these issues further using our case study and compiled accounts of additional *C. johnstoni* attacks on humans in northern Australia.

A.2. Methods

We compiled accounts of *C. johnstoni* attacks that were reported in northern Australia. Accounts were gathered between September 2008 and June 2010 from personal narratives brought to our attention, scientific literature, the internet (primarily online newspapers), and the Crocodile Attack Database (CAD) that was begun in 1971 and is maintained by Wildlife

Management International in Darwin, Northern Territory of Australia (Charlie Manolis, pers. comm.). We included accounts where the attacking species was clearly identified as *C. johnstoni* and where there was no obvious human harassment of the animal prior to attack.

A.3. Results

In addition to our encounter involving two *C. johnstoni*, we recorded ten other accounts of *C. johnstoni* attacks on humans in northern Australia between 1971 and 2009 (Table A.1). This total is likely an underestimate given that three of the attack accounts were collected through chance personal communications (two relayed to the authors and one acquired by C. Manolis second hand [C. Manolis, pers. comm.] and another two through personal experience, meaning that nearly half of the accounts were collected opportunistically rather than being available in the scientific literature or from news sources.

There were an average of 0.3 *C. johnstoni* attacks on humans reported annually in northern Australia between 1971 and 2009 (Table A.1). The first reported attack was in 1988 and the annual number of reported attacks increased to 0.9 between 2000 and 2009. In all cases, the victims were engaged in water activities - swimming, treading water, or floating in an inner tube or on an inflatable mat—at the time of attack. Where gender of the victims was known, numbers were evenly divided between males and females. Crocodile size was estimated in five of the accounts and attacking crocodiles were reported as 1–2 m total length, with 2 m crocodiles being reported as responsible for three of those attacks. Attacks ranged from a quick bite and release to varying degrees of biting persistence until the victim escaped or resisted further bites. Most injuries were restricted to puncture wounds or cuts made directly by the teeth.

Table A.1. Compiled accounts of *Crocodylus johnstoni* attacks on humans in northern Australia, 1971–2009.

Year	Month	Location	Estimated	Victim Activity	Resulting	Victim	Source
1988	N/A	Twin Falls, Kakadu National Park, Northern Territory	N/A	Floating on an inflatable mat.	N/A	N/A	CAD ¹
1990	N/A	Twin Falls, Kakadu National Park, Northern Territory	N/A	Floating on an inflatable mat.	N/A	N/A	CAD ¹
2003	September	Barramundi Gorge, Kakadu National Park, Northern Territory	1.5 m	Swimming.	Puncture wounds on chest; cuts on hand.	Male	ABC 2003
2006	April	Katherine River, Northern Territory	2.0 m	Swimming.	Puncture wounds on back and arm.	Male	Anon. 2006; CAD
2007	January	Ivanhoe Crossing, Kimberley, Western Australia	2.0 m	Swimming.	Eleven stitches on arm; four stitches on neck.	Male	ABC 2007
2008	N/A	Kununurra, Western Australia	N/A	Swimming.	Punctures wounds on arms.	Female	CAD
2008	September	Throssell River, Mt House, Western Australia	2.0 m	Treading water. See case study.	Puncture wounds and soft tissue damage to knee. See case study.	Female	Authors, pers. obs.
2008	September	Throssell River, Mt House, Western Australia	1.0 m	Treading water. See case study.	Puncture wounds on hand and arm. See case study.	Female	Authors, pers. obs.
2009	April	Adcock River, Mornington Wildlife Sanctuary, Western Australia	N/A	Floating in rubber tube with legs in water.	Puncture wounds on leg.	Male	Victim, pers. comm.

¹CAD = Crocodile Attack Database.²We incorporate these accounts of *C. johnstoni* attacks into our analysis because they are included in the CAD and are cited by Anonymous (2006), Caldicott *et al.* (2005), and Crocodile Specialist Group (2008). The original source for these accounts is Lindner (2004), but this reference does not explicitly state that attacks occurred but rather that nuisance *C. johnstoni* were removed from this site.

A.4. Case Study

The authors' *C. johnstoni* attacks occurred on 17 September 2008, along a remote section of the Throssell River in the Kimberley Region of Western Australia (17.43°S, 126.05°E). September is the dry season and the river was divided into a series of water holes. There was a high density of *C. johnstoni* along the river, but the water hole where the attack occurred had no visible individuals on the bank or at the surface of the water. The water hole was ca. 100 m x 20 m and contained deep, murky water. The bank was steep on both sides with boulders on one end of the river bed and a shallow bank adjoining the river bed on the other end. There was dense vegetation and a steep bank along the side of the hole where the authors entered the water.

Around noon KNH entered the water with a splash and was followed about a minute later by AS. Moments after the second splash, KNH headed toward the bank along her previously clear path. She swam into the broadside of a crocodile. She stopped momentarily, then proceeded slightly to the left of her previous path. The crocodile circled and approached KNH from her right side, attacking at a sideways angle from the front and biting her left knee. KNH tried unsuccessfully to pull the jaws off her knee with both of her hands. KNH released the jaw to reach for an assisting hand offered by AS and the crocodile attempted a death roll. KNH successfully resisted and kept her head above water. KNH returned to the bank with the crocodile where both authors identified the species as *C. johnstoni* when the head was lifted out of the water and as being 2 m long (total length). AS gouged one of the *C. johnstoni*'s eyes until it released the knee.

Before KNH exited the water, a second crocodile bit her right arm. KNH freed herself by thrusting her arm down forcefully while twisting it to one side. This crocodile was ~1 m long and was identified as *C. johnstoni* based on shape and size of the teeth puncture wounds. Identification of the second crocodile was further supported by the abundance of this species along the river and no evidence suggesting the presence of *C. porosus*, which local people (pers. comm.) insisted do not occur in the area. Combined injuries from the two attacks included puncture wounds on both hands (Fig. A.1), the right arm, and around the left knee (Fig. A.2).

The left knee also sustained soft tissue damage including a small meniscus tear, sprains, and strains.



Figure. A.1. Hand and arm wounds from *Crocodylus johnstoni* less than an hour after attack.



Figure. A.2. Leg wounds from *Crocodylus johnstoni* five days after attack

A.5. Discussion

For many years, much attention has been focused on understanding and preventing *C. porosus* attacks on humans (e.g., Caldicott *et al.* 2005, Crocodile Specialist Group 2008, Gruen 2009). Little attention has been paid to the dangers of *C. johnstoni*, no doubt because of the prevailing notion that this species is harmless (e.g., Crocodile Specialist Group 2008; Webb and Manolis 2007). To the contrary, our case study, backed up by other reports we have gathered, indicates that *C. johnstoni* are capable of attack resulting in serious injury.

Available data indicate that *C. johnstoni* attacks are not as common, nor usually as severe, as *C. porosus* attacks. From 1971 to 2009 there have been an average of 0.3 reported accounts of *C. johnstoni* attacks on humans per year compared to 1.95 average accounts reported per year for *C. porosus* (C. Manolis, pers. comm.). There are no known cases of human fatality from *C. johnstoni* compared to 25 recorded cases from *C. porosus* between 1971 and 2009 (C. Manolis, pers. comm.). Nevertheless, given the apparently limited reportage, acceptance, and recording of *C. johnstoni* attack accounts, one must wonder how many other attacks have occurred and are not known. In our data set there is a suggestion of an increase in the number of *C. johnstoni* attacks on humans in the last decade. This may indicate an actual rise in the number of attacks, but may also reflect easier access to more recent attack accounts.

Our analysis of available information suggests that improved data collection and access to that data is needed if information on *C. johnstoni* attacks are to be available and useful for both understanding this species' biology and for informing public safety. The IUCN Crocodile Specialist Group's recommended repository for crocodile attack information in Australia is Wildlife Management International's Crocodile Attack Database (CAD). Given that only a third of the attacks compiled here were also in the CAD, this resource appears to be severely underutilized with respect to *C. johnstoni*. While not an unusual situation for data bases of this sort (Fergusson 2002), it remains troubling. One problem is that the data base is not easy to find. Google searches using reasonable search criteria are unable to find a match within the first ten pages of search results. In addition, there is no online data sheet for easy submission and data

contained within the CAD are not readily available online. Equally critical is the encouragement of reporting in the first place. Our experience and findings suggest that *C. johnstoni* attacks deserve more initial credibility and reportage of their details needs to be encouraged. Whether there has been an actual increase in the number of *C. johnstoni* attacks in the last decade or not, the threat of more attacks in the future is real. The numbers of people visiting remote areas continues to rise as improved technology and infrastructure make more challenging locations increasingly accessible. Since *C. johnstoni* have been observed to be less wary of humans and more prone to aggressive displays in areas where they are not regularly exposed to humans (Webb 1985), increased visitation to remote areas could increase the number of attacks. Attacks may become more frequent across this species' range regardless of remoteness as human populations rise, increasing the probability of negative encounters. Clearly outlined safety guidelines exist for *C. porosus* (e.g., Queensland Government 2008). Similar guidelines should be developed and publicized for *C. johnstoni*. However, little is definitively understood in order to undertake such a task. Improved data will be needed to assess the triggers for *C. johnstoni* attack. The only clear evaluations from the data set compiled here is that all victims were in the water at the time of attack and there is no apparent gender bias. It appears that larger *C. johnstoni* are more prone to attack and that attacks are more likely to occur in April or September, but these conclusions are not much more than indicative. Standardized data collection is necessary to limit gaps in the data set and to ensure that the data being collected is useful for understanding *C. johnstoni* attack triggers.

We emphasize the importance of documenting all *C. johnstoni* attacks in a standardized, easily accessible format. Acquiring such data will require an educational campaign to alter the perception that *C. johnstoni* are harmless, to one of recognizing their potential to attack and the need to report such incidents. Future research should pay discerning attention to the details of each recorded attack to increase our understanding of *C. johnstoni* attack triggers. This information is essential to understanding the biology of *C. johnstoni*, improving its conservation and management and, as we have shown in this paper, human safety.

A.6. Acknowledgments

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