



MONASH University

*Life-history variation in a tropical cooperative bird: Ecological
and social effects on productivity*

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Abstract

Reproduction and survival are two fundamental traits that define an individuals' lifetime. Life-history variation within individuals can be related to individual differences on balancing reproduction and survival against the constraints imposed by the physical and environmental conditions they experience. Since individuals vary widely within and between populations in respect to life-history traits, this variation transcends individuals, and life-history strategies differ between species. Understanding the selective pressures that affect individuals will offer an insight on what limits each species' life-history strategy. Here I focus on the ecological and social forces that affect reproduction of the cooperative breeding purple-crowned fairy-wren *Malurus coronatus*, a tropical species that is located at the slow-life history end of the continuum. Using ten years of data from individual longitudinal stories, I analyse many aspects of reproduction: what are the environmental cues that trigger timing of breeding, how much do these environmental variables alone or in combination with social and other ecological conditions influence the final outcome of reproduction and what strategies do pairs use to minimise losses produced by external factors. I demonstrate that *Malurus coronatus* has a fine-tuned mechanism to time breeding cycles with rainfall and that rainfall also determines the quantitative output of successful nest attempts. However, means and extremes of rainfall and temperature have different antagonistic effects that directly or indirectly decrease reproductive success, affecting reproductive success by flooding, increased predation, reduced egg hatchability or lower offspring survival. To overcome such losses, pairs should invest in nest defence and brood rearing, and I test whether this could be improved as a result of long-term partnerships. However, I found that retaining the same partner does not increase productivity. Motivated by this lack of benefits of staying together, I analysed if an adaptive response was to change partners (divorce) if opportunities are available. Divorce is driven by females taking breeding positions in higher quality territories, however this does not lead to

immediate reproductive improvements. More generally, high quality territories (with more vegetation cover) are consistently identified as key factors associated with increased productivity by decreasing the likelihood of nest failure and recruiting more fledglings, which confirms previous research on this species and highlights the importance of “real estate”. All findings in *Malurus coronatus* could possibly be commonplace in other tropical species that occupy year-round territories and are exposed to similar environmental selective pressures. These findings increase what is known for tropical species with a slow-life history strategy, data that is currently scarce. Moreover, my research highlights some potential threats of climate change, in which adaptive responses might not be enough to ameliorate negative impacts due to the slow-pace of reproduction in this species. The importance of habitat quality on reproductive success suggest that the preservation of healthy habitat would be crucial to guarantee this species survival.

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

Publications during enrolment

Thesis including published works General Declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes one original paper published in a peer reviewed journal and three unpublished publications. The core theme of the thesis is the Ecological and Social factors that affect productivity in a tropical bird. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the candidate, working within the School of Biological Sciences of Monash University under the supervision of Dr Anne Peters.

The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of all chapters my contribution to the work involved the following:

Thesis chapter	Publication title	Publication status	Nature and extent (%) of students contribution
1	Fast response to rainfall connects the timing of breeding to food abundance and reproductive output in a tropical bird	In preparation	The candidate collected and interpreted most of the data (90 %). Primary author

2	Contrasting effects of climate means and extremes on nest failure and productivity in an endangered tropical bird	In review	The candidate collected and interpreted most of the data (90 %). Primary author
3	Limited benefits of mate retention for productivity in a tropical passerine	In preparation	The candidate collected and interpreted most of the data (90 %). Primary author
4	Incest avoidance, extra-pair paternity and territory quality drive divorce in a year-round territorial bird	Published	The candidate collected and interpreted most of the data (90 %). Primary author

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Student signature:



Date: 15-10-2016

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the student and co-authors' contributions to this work.

Main Supervisor signature:



Date: 15-10-2016

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Preface

This thesis contains an introduction, four data chapters and a final discussion. Each data chapter constitutes an independent manuscript and its content is formatted according to the requirements of a particular journal. Amendments have been done in format of references, tables and figures in order to combine all chapters. Since each chapter is intended as an independent publication, some repetition of information is found. Chapter four has been published in the journal Behavioral Ecology (Hidalgo Aranzamendi et al. 2016) and it is referred to as Chapter 4 throughout the document. Chapter two has been submitted to the journal Functional Ecology (Hidalgo Aranzamendi et al. *under review*) and it is cited as Chapter 2 throughout. The other 2 chapters are in preparation for submission and referred to by their respective number throughout the document.

This thesis work is my own. All contributors are listed as co-authors including supervisors.

Introduction

Background

Reproduction and survival are fundamental life-history traits that outline an individual's lifetime (Williams 1966, Stearns 1992, Roff 1993). Selection is constrained because reproduction and survival cannot be maximized simultaneously; instead both aspects require a constant trade-off in allocation of resources and eventually each individual does this differently throughout its life (Williams 1966, Partridge and Harvey 1985, Hille and Cooper 2015). Since some individuals are better than others in finding territories, partners or just surviving in general, such differential allocation is reflected in a large variation between individuals' reproductive output (van de Pol 2006). Individuals vary widely within and between populations with respect to life-history traits, and ultimately this variation transcends individuals, and life-history strategies differ between species (Stearns 1992, Ricklefs and Wikelski 2002).

The pace-of-life of a species is a composite of several traits that are the product of life-history trade-offs that individuals face (Hille and Cooper 2015). It has been suggested that each species falls along a continuum going from a slow pace-of-life to a fast pace-of-life strategy (Wikelski et al. 2003, Reale et al. 2010). In birds, most of our understanding of life-history processes comes from the northern hemisphere, where most species fall at the end of the fast continuum and have a reproduce-fast, die-young strategy (Martin 1996). In contrast, species with a slow pace-of-life have: small clutch sizes (Martin 1995b, Stutchbury and Morton 2001), longer incubation and nestling periods (Ricklefs 1969, 1976, Styrsky et al. 2005), prolonged parental care (Russell 2000, Hille and Cooper 2015), low growth rates (Wiersma et al. 2007, Reale et al. 2010), high philopatry (Reale et al. 2010), high juvenile and adult survival (Ghalambor and Martin 2001), late sexual maturation (Russell 2000) and delayed

senescence (Møller, et al. 2007). It is believed that most tropical species are found closer to the slow pace-of-life end (Martin 1996, Stutchbury and Morton 2008, Møller, and Liang 2013). Since reproduction at the individual level eventually determines population dynamics, and thereby affects a species' evolutionary potential and its conservation, understanding the slower pace-of-life of tropical species constitutes a major contribution to a core aspect of life-history theory (Roff 1993). To understand this at the species level, and its implications in population biology, it is important to analyse selective pressures that constrain trade-offs between traits influencing productivity at the individual level.

The slow pace-of-life strategy of tropical species has been attributed to several selective pressures that include: high rates of nest predation (Martin and Briskie 2009), lack of a pronounced peak in food abundance, reduced seasonality and large unpredictability of the environment (Ricklefs and Wikelski 2002), high density of predators (Martin 1995b, 1996), diseases (Reale et al. 2010) (ecological drivers) and relationships within social and family groups (Ricklefs and Wikelski 2002) (social drivers). Although these factors potentially explain life-history traits of a slow pace-of-life, no consensus has emerged concerning the mechanisms that constrain time and energy allocation to life-histories (Ricklefs and Wikelski 2002) and this is mostly due to lack of breeding biology data on tropical species (Martin 1996, 2015, Russell 2000, Stutchbury et al. 2007, Møller, and Liang 2013).

Tropical cooperative breeders offer the opportunity to test several hypotheses proposed to explain productivity of slow-paced species. Cooperatively breeding birds, a group disproportionately represented in the southern hemisphere and in the tropics, are long-lived animals in which trade-offs between reproduction and survival are played out at a particularly slow pace (Cockburn 1998, Koenig and Dickinson 2004, Feeney et al. 2013). Ecological factors, especially environmental variation, has been proposed to be an important driver explaining the occurrence of cooperative breeding (Jetz and Rubenstein 2011). In here,

environmental uncertainty and resource availability (density of breeding sites and territory quality) drive temporal variation and exert selection pressures on cooperation (Walters 1990, Komdeur 1992, Jetz and Rubenstein 2011). Moreover, cooperative breeders delay reproduction until they inherit a breeding position or a vacancy arises elsewhere (Koenig and Dickinson 2004); this delay in reproduction is compensated by increased longevity (Cockburn 1998, Hatchwell and Komdeur 2000). Since these species are found in highly saturated environments surrounded by relatives, they face stringent constraints on movements and pairing opportunities (Cockburn 1998, Hatchwell and Komdeur 2000). These demographic characteristics combined, make them a good system to explore how ecological or social effects determine variation on individuals' decisions on reproduction that might affect survival of those individuals (Stearns 1992, Roff 1993, Martin 1995a).

Thesis aim

In this thesis I study the purple-crowned fairy-wren, a cooperative breeder species found in the monsoonal tropics of Australia, to disentangle how ecological and/or social factors determine variation on individual productivity. This information will be relevant to identify possible threats that jeopardize this bird, since this species has an endangered status.

For this, I used data from a long-term study (2005-2015), in which hundreds of individuals were followed from birth until death. Over those ten years, social and ecological aspects of purple-crowned fairy-wrens' lives were recorded, such as, data for breeding performance, dispersal, survival, territory quality, and environmental climatic factors.

Study species

The purple crowned fairy-wren *Malurus coronatus* belongs to the genus *Malurus*, an endemic Australian-Papuan group (Rowley and Russell 1997). In this part of its distribution, purple-crowned fairy-wrens exclusively occupy territories linearly aligned along water courses and with dense vegetation of a palm-like species *Pandanus aquaticus*. (Rowley and Russell 1997, Kingma 2009, 2011a). Here, each all-purpose territory is occupied year-round by one dominant pair, which are the only ones that reproduce, and are sometimes accompanied by a group of subordinates (helpers) varying from none to 10 (Kingma et al. 2009, 2010). Natal dispersal in this species is female biased, although some females remain philopatric (Kingma 2011b). Movement away from watercourses and dispersal outside river vegetation, or between catchments, has never been recorded for this species (Skroblin et al. 2014).

Unlike other congeners, purple-crowned fairy-wrens have low rates of extra-pair paternity (<6%, Kingma et al. 2009, 2013). Breeding in this population has been recorded year-round, with one marked peak over the wet season (Dec-Mar) and another variable peak at the end of the dry season (Aug-Oct) (Peters et al. 2013).

The subspecies found at our study site, *Malurus coronatus coronatus*, has suffered declines in their distribution and density as a result of degradation of riparian habitat (Skroblin 2012) and to date, it is listed as endangered by the Environment Protection & Biodiversity Conservation Act of Australia (2015).

Field work

The study population is located along Annie Creek and the Adcock River (17° 31'S 126° 6'E) in Mornington Wildlife Sanctuary, a protected area managed by the Australian Wildlife Conservancy since 2004.

The long-term study of this population started in 2005 and until 2010, all birds were captured and banded. During these years, breeding attempts were followed in detail (Kingma 2012). All natal and breeder dispersal events were recorded by weekly censuses in the study site. Since 2010 until 2015, two yearly censuses were conducted in May-June and November after the main two breeding peaks.

All protocols were approved by the ethics committees of the School of Biological Sciences at Monash University (BSCI/2011/28) and the Max Planck Institute for Ornithology under national and international legislation for animal use in research. All research was approved by the Western Australian Department of Environment and Conservation and by the Australian Wildlife Conservancy (AWC).

Outline of thesis

Understanding which ecological and/or social factors determine variation on individual productivity of purple-crowned fairy-wrens is the central theme of this thesis. Optimal individual decisions include choosing the best time to breed, best age to breed, and best mate to breed with, all of which influence reproductive outcomes (van de Pol 2006). Nevertheless, individual's strategies may be constrained, and in my thesis, I explore these aspects trying to understand benefits of, and constraints on, individual strategies for reproduction, by testing ecological and social factors that have been proposed as the main drivers of a slow pace-of-life strategy. My thesis is partitioned into four data chapters, each of which discusses a specific topic. The first part of the thesis (Chapter 1 and 2) is focussed on ecological drivers of reproductive output, and the second part (Chapter 3 and 4) on social drivers that influence reproductive output at the individual level. Finally, I discuss the main findings of all chapters

highlighting the main environmental factors that are affecting productivity in this species and eventually how this influences population dynamics.

In **Chapter 1**, I explore the climatic factors that determine timing of breeding and the consequences of timing on two aspects of productivity: clutch size variation and survival of eggs and offspring. It has been proposed that the tropics lack strong seasonality when contrasted with temperate regions, and cues that tropical species follow might differ from recognizable cues in those striking seasonal environments (e.g. day length) (Hau et al. 1998, 2004, 2008). Therefore, identifying the cues for reproduction for tropical species would help us to understand variation in components of the environment (e.g. food supply, predators) that affect reproductive cycles (Grant et al. 2000, Wikelski et al. 2000, Schaper et al. 2012). Such cues are likely to be tightly linked to the climatic characteristics of the region (Hau et al. 2008). Using a recently developed integrative modelling approach I analysed 685 nesting records of 171 pairs in our study population and determined the relationship climate - food availability - reproduction for the purple-crowned fairy-wren. In this chapter I showed how climatic variation triggers reproduction. How climate affects the outcome of reproductive attempts is topic of the next chapter.

Climate variation is generally assumed to be an important determinant of productivity and survival in tropical species and cooperative breeders (Jetz and Rubenstein 2011, Oppel et al. 2013). In **Chapter 2**, I focus on how much the outcome of reproductive attempts (i.e. failure or success in nest attempts) is determined by two aspects of climate variables (means and extremes). Species responses to different components of the same climatic variable - means versus extremes – are needed to understand effects of climate variability, and such responses and the interaction with habitat quality have to be analyzed simultaneously. Such information is critical, because it is likely that climate variables and thresholds affecting the biology of tropical species cannot be extrapolated from findings in other latitudes. For instance, rainfall

constitutes a major climatic feature that defines seasonality in the tropics and a determinant of the biological cycle of tropical species, rather than temperature, as is common in temperate latitudes. Using an integrated approach, I combined almost 700 detailed nest records obtained over 5 years with detailed information on climatic conditions they experienced and habitat quality. I analyzed the effects of means and extremes of temperature and rainfall on the outcome of all stages of the nesting cycle. This chapter highlights the complex effects of environmental variation upon reproduction and how low reproductive success comes about in tropical species.

Chapter 1 and 2 focussed on the major ecological factors affecting reproduction (climate, habitat quality, and predation) and their impact in this population. Since variation in reproduction is constrained by trade-offs between survival and individuals' investments in reproduction (Roff 1993), it is necessary to consider factors at the individual level that will also determine reproduction. In **Chapter 3**, I analysed how individual and social breeding history affect productivity. Effects of the length of relationships and breeding experience on reproduction have been largely explored in different life-histories (Black 2001, Naves et al. 2007). Species establishing long-term pair bonds are predicted to do so, to increase reproductive success over time (Black 2001) and that improvement occurs not only with breeding experience *per se*, but also with increasing pair bond duration (Martin 1995a, Fowler 1995). The effects of pair bond duration on productivity have been little explored in species from tropical latitudes, despite the fact that several tropical species form such long-term pair bonds (Stutchbury and Morton 2001, Tobias et al. 2016). I explore the effects of pair bond duration on reproduction, using the breeding history of 194 pairs with known pair bond duration and known breeding experience. The benefits of long pair bonds might be absent or constrained in tropical cooperative species and explained by other ecological

factors, because cooperative breeders also experiment saturated environments with large constraints in social partner choice.

The adaptive benefits or limitations that social partner choice have on successful reproduction can be also analysed by studying the paths of formation and dissolution of relationships. In **Chapter 4**, I focus in the causes and consequences of divorce. Despite the obvious benefits of staying in a long-lasting pair bond, divorce is common in monogamous species (Choudhury 1995). Only recently, it has become accepted that this behaviour is an adaptive strategy to improve fitness (either reproduction or survival) (Culina et al. 2014). For species that maintain pair bonds year-round, the limited availability of breeding positions presumably constrains the opportunities for initial mate choice as well as partner change, but the ecological and demographic drivers of divorce remain largely unknown. Investigating divorce in purple-crowned fairy-wrens, allowed me to test several hypotheses in relation to the full range of ecological and social external covariates and the impact that divorce has on reproductive success of individuals.

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PART B:

Declaration for Thesis Chapter 1

Declaration by candidate

In the case of Chapter 1, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The key ideas, data collection, data analysis, lab work and writing of the manuscript were my responsibility.	90

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution
Anne Peters	Assistance with writing manuscripts, design of hypotheses, data collection, interpretation of results, feedback on thesis
Michelle L. Hall	Assistance with writing, data collection, interpretation of results.
Sjouke A. Kingma	Assistance with writing manuscripts, data collection, interpretation of results.
Martijn van de Pol	Assistance with data analysis, interpretation of results.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work.

Candidate's Signature

Date: 15-10-2016

Main Supervisor's Signature

Date: 15-10-2016

Chapter 1

Fast response to rainfall connects the timing of breeding to food abundance and reproductive output in a tropical bird

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Abstract

Changes in climate are causing changes in the seasonal timing of many phenomena in the natural world. Phenological mismatches due to global warming are well known from northern temperate regions, but such effects are much less well understood in tropical and southern regions. We used a new modelling approach to identify the critical climate signals that trigger two biological responses: nest initiation by a tropical insectivorous bird, and increases in arthropod abundance (representing its food). We then assessed how these critical climate signals affected breeding success. Birds initiated nesting in response to cumulative rainfall in the month prior to egg-laying, and no other climate variable predicted nest-initiation. Arthropod abundance also increased in response to rainfall only, and a slower response meant that the peak coincided with peak food demand of fledglings. The rapid nest-initiation response of females to the same climate signal that triggers increases in arthropod abundance effectively allows females to time their breeding to match optimal food supply for offspring. Indeed, the

amount of rainfall during the critical window predicted reproductive output. Knowledge about the climate signals driving variation in food availability is essential to predict the effects of climate change on breeding success globally.

Key words: phenology, tropical, ecological mismatch, multi-brooded, climate change

Introduction

The seasonal timing (phenology) of natural phenomena such as plant growth and animal breeding are driven by seasonal changes in climate cues such as daylight, temperature and precipitation (Hughes 2000, Schwartz 2003, Møller et al. 2008). Recent changes in global climate are causing changes in the breeding phenology of taxa that reproduce seasonally. This has been particularly noticeable for species living in northern temperate latitudes that use increasing temperatures as a cue to start breeding (Crick et al. 1997, Hughes 2000, Visser et al. 2004, 2006b, 2008, Schaper et al. 2012). For instance, birds have advanced their laying dates as a response of such increase (Both and Visser 2001, Dunn and Winkler 2010), and these widely observed patterns constitute the best documented evidence of climate change on wild animals (Root et al. 2003, Dunn and Winkler 2010).

The climate cues driving the seasonal timing of breeding in tropical birds are much less well understood than those of the north-temperate zone, and little is known about the response of tropical species to altered climate. This is mostly due to lack of detailed phenological data and the fact that species-specific climatic factors that trigger breeding are poorly understood (Charmantier and Gienapp 2014). Unlike species from temperate environments, the breeding schedules of tropical birds can vary considerably. Breeding activity could be highly predictable (e.g. Spotted Antbird, Hau et al. 1998), or breeding can be opportunistic with high levels of flexibility (e.g. Zebra Finches or Galapagos Finches, Grant et al. 2000, Wikelski et al. 2000, Hau et al. 2004). Although day length changes seasonally in near-equatorial

habitats, the amplitude of this variation is much reduced closer to the equator (Hau et al. 2008). Similarly, ambient temperature in near-equatorial tropical habitats is subjected to less variation (Wikelski et al. 2000, Hau et al. 2004), thus these factors are unlikely to be the main cues for breeding (but see Hau et al. 1998). Instead, rainfall is likely to be important (Hau et al. 2008).

Rainfall, especially where it defines seasonality (monsoonal tropics) or is the limiting resource (arid zone), has been proposed as the most likely strong determinant of breeding calendars for many tropical species (Wingfield et al. 1992, Hau 2001, Shine and Brown 2008), predicting food peaks better than day length (Grant et al. 2000). Although tropical rainfall might have a mostly predictable annual schedule (Hau et al. 2008), it has wide local variability and relatively low predictability of frequency and intensity (Shine and Brown 2008, Mohtadi et al. 2016). Moreover, as one consequence of global change, the intensity and timing of tropical rainfall have been predicted to change dramatically in the upcoming decades (Lehmann et al. 2015) and the impact that such changes might have on the reproductive calendar of tropical species remains unknown (Chambers et al. 2013).

It is also uncertain if changes in rainfall could cause a desynchronization between breeding and seasonal peaks of arthropod prey abundance, as it occurs in temperate latitudes (when consumer and prey are not reacting to the same cue and/or time window, e.g. Both and Visser 2001, Chambers et al. 2013, Visser et al. 2004, 2006a, Schaper et al. 2012). However, no conclusions can be drawn about decoupling of breeding phenology and food abundance in the tropics from extrapolating changes in temperate regions (Stenseth and Mysterud 2002, Hilden et al. 2012). For instance, it is relatively unexplored how food abundance fluctuates in the tropics and how females match their breeding calendar to such fluctuations, how females responsiveness vary and if so, what are the consequences for productivity (but see Grant et al. 2000). Alternatively, the importance of timing might not be so relevant for tropical species,

since they are multi-brooded and might be less sensitive to shifts in the timing of climatic cues (Dunn and Moller 2014).

Here we quantify the environmental triggers of breeding and food phenology of a resident tropical bird with a flexible breeding calendar. To do so, we use five year data from a detailed individual-based study on the purple-crowned fairy-wren, an insectivorous passerine species of the monsoonal tropics (Rowley and Russell 1997, Peters et al. 2013). This is a sedentary cooperatively breeding bird that depends exclusively on the arthropod prey found in their year-round territories. First, we use a recently developed systematic approach (van de Pol et al. 2016) to identify the critical climatic factors and time frame that predict female nesting activity and arthropod abundance (a proxy for food availability). Subsequently, we examine the consequences of the identified climatic cues on reproductive output.

Methods

Study species and site

A population of purple-crowned fairy-wrens *Malurus coronatus coronatus* was monitored at Australian Wildlife Conservancy's Mornington Wildlife Sanctuary, located in the monsoonal tropics of northwest Australia (17°31' S, 126°6' E). Birds in our study population occupied year-round territories along ~15 km of river along Annie Creek and Adcock River (Kingma *et al.* 2009) and were individually colour banded and followed throughout their lives. Purple-crowned fairy-wrens are riparian habitat specialists, and territories are associated with the evergreen palm-like *Pandanus aquaticus*. Each territory is defended by a dominant pair, sometimes accompanied by a group of subordinates which are mostly (~60%) offspring of the dominant pair; group size ranges from 2 to 10 birds. Only the dominant pair reproduces but subordinates participate in offspring care, thereby improving reproductive success and breeder survival (Kingma et al. 2009, 2010). In our population breeding can occur in every month of

the year, but there are peaks during and after the wet season (Dec-Mar) and often, but not always, a peak at the dry season (Sep-Oct) (Rowley and Russell 1993, Peters et al. 2013, Fig S1).

Nesting

Between July 2006 and November 2010 we recorded 665 nesting attempts (477 found before eggs, 143 with eggs and 45 with nestlings). Open cup nests are built exclusively by the dominant female over a period of approximately 10 days prior egg-laying (Hall and Peters 2009). Nest material included flood debris, pieces of *Pandanus* leaves (36%), dried grass, stems and rootlets (21%) forming a coarse outer layer lined with a basket of finely woven material (M. Hall unpublished data). Nest never contained feathers and most nests were built in *Pandanus* (96% of 743 nests). Laying date and clutch size (2-4 eggs) were determined by checking nest contents at three-day intervals after building was complete until clutch completion. Information on reproductive output was analysed only for nests with known clutch size. Incubation lasts ca. 12 days (Rowley and Russell 1993).

When nestlings were 7 or 8 days old, they were banded with a unique combination of coloured bands and one numbered band, weighed and a blood sample taken for parentage analysis and sex determination (Kingma et al. 2011a). Nestlings usually left the nest 12 or 13 days after hatching ($n = 16$ nests; unpubl. data), and after the expected fledging date, we searched the nest area to locate the fledglings. Territories were visited weekly to confirm the presence of fledglings, which remain with the family group. To have an estimation of post-fledgling provisioning time, we conducted 20-minute focal observations of fledglings ranging in age from 2-16 weeks post-fledging and recorded when fledglings were fed by group members or foraged independently. The number of fledglings surviving up to 6 weeks after fledging (~9 weeks old) were quantified for successful nests (those not lost due to predation or flooding).

Environmental variables

Rainfall and temperature. Our study site receives 89% of the total annual rainfall (average \pm SD = 772 ± 92 mm) during the ‘wet season’ from December to March. There is considerable inter-annual variation in the onset and intensity of the wet and dry seasons (Brown and Shine 2006, see also Fig. S1). Daily records of local rainfall were obtained by a weather station at our study site since 2004 (Australian Bureau of Meteorology (BOM) weather station 002076, Fig.1). Temperatures are generally high – monthly mean maxima range from 28 to 42°C (in November), and monthly mean minima range from 13 (in June) to 32°C, see Fig. S1). Daily records of temperature for Mornington Wildlife Sanctuary (our study site) were only available for 30 months (January 2008-July 2010) and therefore we obtained long-term daily temperature data from Fitzroy Crossing (BOM weather station 003093, 18.19°S, 125.56 °E, ~ 95 km SW from our study area) (Fig. S1). Daily temperature at Fitzroy Crossing is strongly correlated with temperature data obtained at our study site (Spearman Rho = 0.94, $p < 0.001$, $n = 30$ months).

Arthropod abundance. This was recorded monthly from September 2007 until June 2010 (Fig.1). The exact diet composition for purple-crowned fairy-wrens is unknown, but all fairy-wrens are generalist insectivores that eat a wide taxonomic range of small arthropods (Rowley and Russell 1997). After an initial sampling in all territories, six representative territories were chosen by their low, medium and high abundance of arthropods (3 sampling sites at each river). Each sampling was performed at the middle of each month in those representative territories. In total, 3 sets of 15 sweeps were done in each territory (midpoint and two other points separated 10 m upstream and downstream; for details see Kingma et al. 2011a). The monthly

average of summed length of all arthropods was used as an indicator of food abundance (Kingma et al. 2011a).

Territory quality. *Pandanus* cover was quantified as an index of habitat quality of the breeding territory (for details see Hidalgo Aranzamendi et al. 2016). Birds do not occupy areas without *Pandanus* and there is large variation in *Pandanus* distribution between territories (Kingma et al. 2011a). Territories with greater *Pandanus* cover suffer from lower rates of nest predation (Chapter 2). Moreover, territories with greater *Pandanus* cover have more subordinates, indicating that they are more productive or more attractive for subordinates to delay dispersal (Kingma et al. 2011a) and are preferred by females dispersing after divorce (Chapter 4). Number of helpers in a territory was considered an additional component of territory quality, because breeders derive reproductive and survival benefits from larger groups (Kingma et al. 2010, Chapter 2).

Statistical analyses

We analysed the influence of environmental variables on timing of reproduction, female condition, arthropod abundance and productivity in three steps. First, (A) we identified the sensitive time window for various climate variables that could affect: (i) nest initiation at the individual level (start of nest building), (ii) female condition at the individual level (from year-round captures) and a sensitive time window for (iii) arthropod availability (arthropod abundance) for the population. Then, (B) once a sensitive window for each climate variable was identified; we used this time window to find the best supported models that determined the magnitude of the three biological responses. Third, (C) we determined the effect of the identified environmental factors on reproductive output of the nesting attempt (clutch size,

nestling condition and number of recruits). Explanatory variables included were not strongly correlated (all $|r| < 0.58$). All analyses were done in R 3.2.0 (R Core Team 2015).

(A) *Identifying the critical climatic time window.* We used critical climate window modelling (van de Pol and Cockburn 2011) to identify the climatic time window that best predicts biological responses. This approach allows selecting the period in which a biological response is most strongly affected by climate (Bailey & van de Pol 2015). This method also allows distinguishing short and long-lag effects of climate signals that might be acting differentially among individuals when events occur at different times of the year (i.e. relative window, van de Pol & Cockburn 2011, van de Pol et al. 2016). First we identified which climatic windows determined (i) *nesting activity*. Using the software *climwin* and the *slidingwin* function (Bailey & van de Pol 2015), we analysed year-round nesting data using a time-to-event Cox's proportional hazard analysis (Cox's HA) with calendar date of events as a response variable (nesting = 1, not nesting = 0, grouped per two weeks for each pair as the model failed to converge with daily values) in relation to daily climate data. All nesting attempts (failed and successful) of each pair were included. We tested cumulative rainfall (linear and quadratic) and average daily temperature (linear) as explanatory climatic variables (models failed to converge with temperature as quadratic variable and similarly when interactions were included). Models with maximum and minimum daily temperature gave similar results as the average temperature model, and therefore we show results for average daily temperature only. Interactions between dependent variables were first tested in simple GLMMs (not with *climwin*) to avoid convergence issues when running the *slidingwin* simulation. Since no interactions were found, we proceeded to run models without interactions. We tested several cut-off points for time windows (8, 6, 3 and 1 months) and based on those tests, we specified a window up to 75 days backdating from the event of interest for rainfall and up to 180 days for temperature. We used

relative time windows, because the timing of trait expression varies substantially among individuals (i.e. nests can be initiated year-round; for further information on methods see van de Pol et al. 2016). We also included the outcome of previous nest (failed or successfully fledged) and nesting interval in weeks (linear and quadratic) as co-factors, since the likelihood of re-nesting is dependent on these two variables, possibly in a non-linear way (as found for other multi-brooded species, see Oppel et al. 2013). Second, we tried to identify the critical climatic time window that affected (ii) *female condition*, using 5 years of capture data of all dominant females, here we used a generalized linear mixed model (GLMM) including female weight as a response variable in relation to daily climate and with female identity as a random factor. We specified a window up to 180 days backdating from the capture date. Cumulative rainfall (linear and quadratic) and average temperature (linear) were tested as explanatory variables. Finally, we aimed to identify the critical climatic time window that affected (iii) *arthropod abundance*. For this, we analysed year-round arthropod abundance data using a linear model (LM) including monthly arthropod abundance as a response variable in relation to daily climate data. We specified a window up to 180 days backdating from the sample date each month. We tested cumulative rainfall (linear and quadratic) and average temperature (linear) as explanatory climatic variables. Monthly cumulative data for arthropod abundance was available (Sep 2007- Jun 2010) for the entire study area. Using the *plotall* function from the *climwin* package, we visualized information on all fitted climate windows.

(B) *Determining the biological response*. Using the *bestmodel* function, we selected the strongest climate window model based on AICc values, after the simulation identified the critical time window for nest initiation, female condition and arthropod abundance (Bailey & van de Pol 2015). To confirm that our observed results were not product of random chance, we performed a randomization of the data using 5 repeats (Bailey & van de Pol 2015).

(C) *Climatic effects.* Based on the critical time window and climatic parameters identified as important for nest initiation, we tested if the rainfall experienced in the month prior to egg-laying (explanatory variable) predicted quantity and quality of offspring, namely: clutch size, number of fledglings surviving to independence and condition of nestlings. Rainfall was included as a linear and quadratic term and month of the year was included as a continuous linear and quadratic variable (month 1=July) to control for temporal variation in nest success (Chapter 2). Quadratic terms were posteriorly removed if not significant. Two generalized linear mixed models (GLMMs) with Poisson distribution were built for clutch size (count variable, range = 2-4) and number of fledglings that survived until 6 weeks after fledging (count variable, range = 0-4) as dependent variables. Here we excluded nests that failed due to predation or other causes (Chapter 2). Other explanatory variables included were: habitat quality and group size and female identity as random term. Since our dataset includes repeated measures of individuals' reproductive output (clutch size and number of fledglings) across multiple climatic situations, we separated the variance associated with multiple measurements of the same individual in GLMMs into variance associated with measurements of the same individual (within-individual variance) or measurements of individuals from the same area (between-individual variance) (Van de Pol & Wright 2009). All models were first fitted with generalized linear models (GLM) without random terms to test for overdispersion, and we proceeded to include random terms in the models detailed above because data was not overdispersed. To test if the rainfall experienced in the month prior of egg-laying affected nestling condition, a restricted maximum likelihood model (REML) was built including body mass of the birds captured at day 7 (continuous variable, range = 5-10 g) as dependent variable. Explanatory variables were: rainfall and month as linear and quadratic terms (quadratic terms dropped if not significant), habitat quality, group size, sex and time of the day. Nest identity was added as a random term to control for pseudo replication. Within and between female

effects could not be tested here, due to reduced sample size from several nests with complete information on nestling condition for the same females. All continuous variables were scaled and centered. Means (\bar{x}), estimates (β) and their standard error are presented (\pm SE). Sample sizes are shown in tables.

Results

The critical climate window predicting timing of breeding and female condition

Purple-crowned fairy-wrens initiated nests in all months of the year, with seasonal peaks during the wet season and sometimes during the dry season (Fig. 1). At the population level, cumulative rainfall in the month (~from 2 to 24 days) prior to nest initiation was the best supported climatic signal (Table 1), with the best supported models showing a window opening 24 days and closing 2 days before nest initiation (Table S1, Fig. 2), temperature had no effect on the probability of nest initiation ($\beta = -0.14 \pm 0.09$, $p = 0.11$, Fig. S2). Increases in cumulative rainfall in the 3.5 weeks (2-24 days) prior to nest initiation increased the fortnightly probability of nesting (linear effect, Cox's HA, $\beta = 0.07 \pm 0.02$, $p < 0.001$, Table 1), with the effect of rainfall on nest initiation levelling off with high rainfall (quadratic effect, $\beta = -0.01 \pm 0.00$, $p < 0.001$, Table 1).

Individual factors also affected the likelihood of nest initiation. The probability of nest initiation increased with the time since the previous nesting attempt ended (i.e. re-nesting interval) (Cox's HA, $\beta = 0.13 \pm 0.04$, $p < 0.001$) and decreased if the previous nest had failed ($\beta = -0.41 \pm 0.13$, $p < 0.001$) (Table 1). Re-nesting intervals after successful nests were longer and more variable than intervals following failed nests (re-nest interval after successful nests = 20 ± 11 weeks, after failed nests = 5 ± 8 weeks (raw data), t-test, $t = 12.70$, $p < 0.001$).

No climate window was identified to explain female condition: rainfall (GLMM, linear effect, $\beta = 0.01 \pm 0.01$, $p = 0.84$, quadratic effect $\beta = 0.002 \pm 0.001$, $p = 0.10$) and temperature (GLMM, linear effect, $\beta = 0.05 \pm 0.02$, $p = 0.14$).

The critical climate window predicting timing of arthropod abundance

The timing of arthropod abundance depended on slightly longer-term climate parameters than timing of breeding. The best supported model indicated that the timing of greatest arthropod abundance depended on rainfall ~2 months previously, with temperature having no effect (Figs 2 and S2). The best supported models show a window opening 70 days and closing 56 days before the sampling date (Table S1). Greater total rainfall during this critical window (56-70 days before sampling) resulted in increased abundance of arthropods, with an initial strong linear effect of rainfall (LM, R^2 adjusted = 0.41, $\beta = 0.17 \pm 0.04$, $p < 0.001$, Table 1, Fig. 2), and with effect of rainfall on arthropod abundance levelling off with high rainfall values (quadratic effect $\beta = -0.14 \pm 0.01$, $p < 0.001$, Table 1, Fig. 2). The peak in arthropod abundance following rain appears to last up to two months (Figs 1 and S1).

Effect of rain during critical climate window on reproductive output

Clutch size averaged 2.93 ± 0.05 eggs (range 2-4, median = 3) and increased with the amount of rainfall of the month (2-24 days) prior to egg-laying (GLMM, Table 2, Fig. 3a). We found no quadratic effect of rain and this variable was dropped from the model. No other variable influenced clutch size (Table 2). When partitioning the effect of rainfall on clutch size to effects within- and between- females, we found a within-female effect of variation in rainfall on clutch size ($n = 96$ females, 532 capture records, rainfall $\beta = 0.07 \pm 0.03$, $p = 0.02$) indicating that when females experienced more rain they laid larger clutches. We did not find a between-female effect of variation in rainfall with clutch size (mean rainfall $\beta = 0.04 \pm 0.03$, $p = 0.20$).

and other variables also did not influence clutch size (territory quality $\beta = -0.01 \pm 0.01$, $p = 0.87$, group size $\beta = 0.02 \pm 0.02$, $p = 0.34$, month of the year $\beta = 0.01 \pm 0.03$, $p = 0.70$).

Greater rainfall prior to egg-laying tended to be associated with greater recruitment: nests that experienced higher rainfall in the month prior to egg-laying tended to produce more fledglings (GLMM, $\beta = 0.13 \pm 0.07$, $p = 0.07$, Table 2, Fig. 3b). Larger groups tended to recruit more fledglings ($\beta = 0.08 \pm 0.05$, $p = 0.08$) but this was not related to habitat quality or month of the year (Table 2). When partitioning the effect of rainfall on recruitment to effects within- and between- females, we did not find within- or between-female effect of variation in rainfall on number of fledglings (GLMM, mean rainfall $\beta = 0.06 \pm 0.05$, $p = 0.27$, rainfall $\beta = 0.08 \pm 0.05$, $p = 0.14$). Rainfall of the month prior to egg-laying did not explain nestling condition (Table 2).

Effect of arthropod abundance on reproductive output

Arthropod abundance was correlated with the number of fledglings surviving to six weeks at the population level (arthropod abundance in the month of fledgling count with number of recruits in the same month: Spearman Rho = 0.45, $p = 0.007$, $n = 32$ months, Fig. 4).

Discussion

We showed that local climate has a major influence on the seasonal timing of breeding in purple-crowned fairy-wrens and that rainfall, rather than temperature, is a fine-scale predictor of nesting and optimal food supply. To our knowledge this constitutes one of the few examples in which rainfall has been demonstrated to link phenology at two trophic levels: peak biomass of arthropods and breeding phenology of insectivorous birds. Our findings suggest that the rapid response of females to rainfall – the same climate signal that drives increases in arthropod abundance- allows individuals to match the timing of breeding to peak food abundance, thereby increasing production of offspring that need extended parental care.

Rainfall triggers female's response to initiate nesting

It seems that purple-crowned fairy-wren females are directly responding to rainfall (Lloyd 1999, Whitehead and Saalfeld 2000), since they showed a fast response to rainfall, initiating breeding very soon after the start of rain (2-24 days) (Table 1). To test whether the observed pattern was due to some females being better at adjusting their response to climate (i.e. between-individual effects) or if it was a plastic response in which all females tracked the quantity of rainfall in their decision to breed (Van de Pol & Wright 2009). We showed here a within-individual effect on clutch size, indicating that females displayed individual variation in plasticity in the timing of breeding in regards to rainfall. Breeding in response to rain has been demonstrated for several tropical species (Lack 1954, Grant et al. 2000, Houston 2013). Such an efficient response in nesting activity is expected when rainfall is unpredictable, and this is particularly relevant for tropical and sub-tropical species that inhabit arid and semi-arid habitats (Hau et al. 2004, Senapathi et al. 2011, Houston 2013). Although the monsoonal tropics have seasonal rain regimes, the onset and timing of rainfall vary widely among years (Brown and Shine 2006), suggesting that monsoonal species might adjust their breeding to rain similar as species from arid environments (Hau et al. 2004). In here, females timed their nesting to the periods with more food abundance for fledglings, which directly affected productivity.

Females use quantity of rainfall as a cue to anticipate food for offspring: possible physiological mechanisms

Females experiencing more rain during the critical time window laid larger clutches (Fig. 3a), resulting in more recruits (Fig 3b). However, responses to rainfall were mostly quantitative than qualitative, since rainfall of the month prior to egg-laying did not influence nestling condition (Table 2). Such quantitative responses have been also found for species inhabiting

arid environments in Africa, America and Australia (Lack 1954, Lloyd 1999, Grant et al. 2000, Houston 2013). Females seem to use rainfall as a cue to anticipate food for their offspring, since female condition is not related to rainfall on any temporal scale (no climatic window could be identified). A response to rainfall not being mediated by female condition initiating breeding is in agreement with apparent year-round, opportunistic reproduction of female purple-crowned fairy-wrens. Although we lack records of gonadal size, our year-round records of nest initiation on some years but not others, suggest that the physiological mechanisms that birds use to be ready for egg-laying, could be similar to the one of opportunistic breeders in arid environments. In here, the reproductive system of birds stays in quiescence, without being completely shut-down during dry periods until rainfall stimulates reproduction (Wikelski et al. 2000, Hau et al. 2004). Also, probability of repeated breeding was not only determined by rainfall but also by the outcome of the previous nest (successful or failed) and nesting interval (Table 1), thus long periods without breeding after nests were repeatedly unsuccessful, could be directly linked to a decline in rainfall. The effect of rain, in combination with individual determinants on re-nesting, suggests that gonads are never fully regressed. .

Arthropod abundance as key mechanism

Our results show that the peak of arthropod abundance coincides with the period after fledging (Fig. 5, as Houston 2013). This in contrast with species in temperate latitudes in which the time of arthropod peak rather matches the nestling period (Visser et al. 2003, 2006b, Both et al. 2009). The timing matches the long period of parental care that fledglings need, as is common in tropical species (Russell et al. 2000, 2004). Purple-crowned fairy-wren offspring leave the nest three to four weeks after the start of incubation (Fig. 5) and receive most of their food via provisioning until they are ca. 5 to 6 weeks old, after that period they are more likely to find their own food as they age (Fig. S3). In temperate species, the food supplied to nestlings

predicts post-fledgling survival (Naef-Daenzer et al. 2016). Here, we have shown that for a species that requires longer care, it is possible that food supplied to fledglings is key to predict recruitment and juvenile survival. For species with long periods of fledgling dependence (Russell et al. 2000, 2004), matching timing of breeding with fledgling's demand might be more relevant than timing it with hatching. This is supported by the positive effect of arthropod abundance on fledgling recruitment (Fig. 4), which – stochastic catastrophes such as nest predation or inundation excluded - is more strongly affected by post-fledging survival (30% of fledglings survive), than by nestling survival (90% of nestlings survive).

Conclusion

Knowledge of climatic factors driving breeding phenology for tropical and southern hemisphere species is limited. Here we show a tropical species that responds rapidly to rainfall, with no other climatic cue affecting nesting. Although this species lives in a seasonal monsoonal environment, it seems that it has adaptations more similar to species living in arid conditions in their patterns of opportunistic breeding. The lack of explanatory power to predict the direction of shifts in precipitation for the tropics prevents predicting the effects of ongoing climate change on phenology (Chambers et al. 2013). However, the rapid response to rain; the fact that food availability responds to the same cue; the small, multiple broods; and ability to flexibly regulate individual breeding to climate and past breeding success, gives some confidence that phenological mismatches of the type encountered by insectivore specialists in the northern hemisphere (Both and Visser 2001, Visser et al. 2006a, 2006b, 2008, Dunn and Winkler 2010) are less likely to be imminent for such tropical species.

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Table 1. Rainfall in the previous month (2-24 days, linear and quadratic) was the best supported climatic signal influencing the probability of (a) nest initiation, and rainfall of the 56-70 days (linear and quadratic) prior to the sampling date was the best supported climatic signal explaining (b) arthropod abundance. No significant effect of temperature was found on phenology at either tropic level. The probability of nest initiation was affected also by the time since the previous nesting attempt (nest interval) and the outcome of the previous nest (successful or not). Results $p < 0.01$ shown in bold.

(a)Nesting	Predictor	Effect	SE	Z	p
	Rainfall (cm)	0.07	0.02	4.02	< 0.001
	Rainfall (cm) ²	-0.01	0.00	-4.09	< 0.001
	Temperature	-0.14	0.09	-1.61	0.11
	Nest Interval	0.13	0.04	3.13	0.001
	Nest Interval ²	-0.01	0.01	-3.80	0.001
	Previous nest successful (yes/no)	-0.41	0.13	-3.12	0.001

(b)Arthropod abundance	Predictor	Effect	SE	Z	p
	Rainfall (cm)	0.16	0.01	2.09	<0.001
	Rainfall ² (cm)	-0.14	0.01	-2.83	<0.001
	Temperature	13.81	17.49	0.79	0.44

Table 2. Effects of rainfall in the month prior to egg-laying (identified as the critical time window for nest initiation, Table 1) on reproductive output in purple-crowned fairy-wrens. Dataset includes first and re-nesting attempts. Results of generalized linear mixed models (a-b) with Poisson distribution and restricted maximum likelihood model (c) with normal distribution. Random factors did not contribute to variance in the models. Shown are sample sizes, model estimates, their standard errors (SE), z-value and significance, results $p < 0.01$ indicated in bold.

Response variable	(a) Clutch size (2-4)				(b) Number of fledglings (0-4)*				(c) Nestling condition (body mass, g)**			
Number of observations	n= 532 nest (171 pairs)				n=192 nests (111 pairs)				n=357 nestlings (160 nests)			
Fixed effects	Estimate	SE	z-value	p	Estimate	SE	z-value	p	Estimate	SE	z-value	p
Rainfall of the month prior-to egg laying	0.07	0.02	2.63	0.002	0.13	0.07	1.84	0.07	-0.10	0.10	-1.04	0.30
Habitat quality	-0.01	0.01	-0.12	0.89	-0.01	0.01	-1.02	0.31	-0.01	0.08	-0.15	0.88
Group size	0.02	0.02	0.96	0.34	0.09	0.05	1.76	0.08	0.11	0.09	1.26	0.21
Month (1=July)	0.01	0.03	0.37	0.71	-0.04	0.09	-0.42	0.67	0.08	0.09	0.85	0.40
Time of the day	n.a.	-	-	-	n.a.	-	-	-	-0.01	0.08	-0.11	0.91
Sex ***	n.a.	-	-	-	n.a.	-	-	-	0.25	0.07	3.49	< 0.001

* non-failed nests only (i.e. excluding nests lost to predation, flooding and other causes of total nest failure).

**body mass on day 7.

*** estimate is male relative to female (males are larger)

Figure 1. The number of territories initiating nests (black columns) is a response that follows cumulative rainfall of the previous month (blue line). Arthropod abundance follows rainfall with approximately 2 month-lag (green line). The number of fledglings surviving 6 weeks after fledging (orange column) peaks at the same time as arthropod abundance. Arthropod abundance represented by average of summed length of all arthropods in mm for Sep 2007 to Jun 2010.

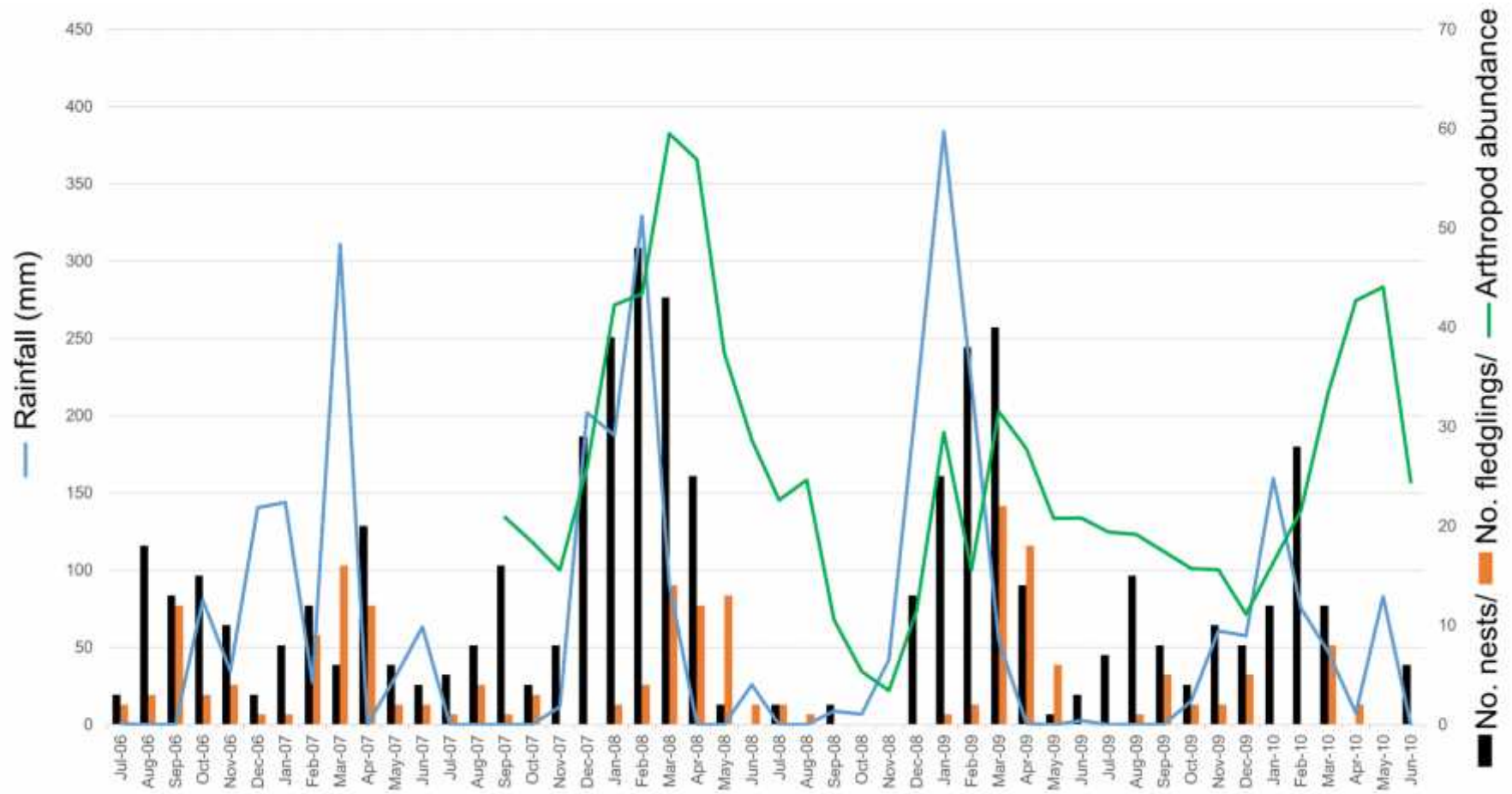


Figure 2. Model support for best window (lower $\Delta AICc$) for rainfall in relation to (a) nesting initiation (2 - 24 days) and (b) arthropod abundance (56 - 70 days). Window open (y-axis) and window close (x-axis) in days before timing of nest initiation or measurement of arthropod abundance. Models with the lowest $\Delta AICc$ (red and pointed by arrow) are the best supported and indicate the number of days of a relevant window.

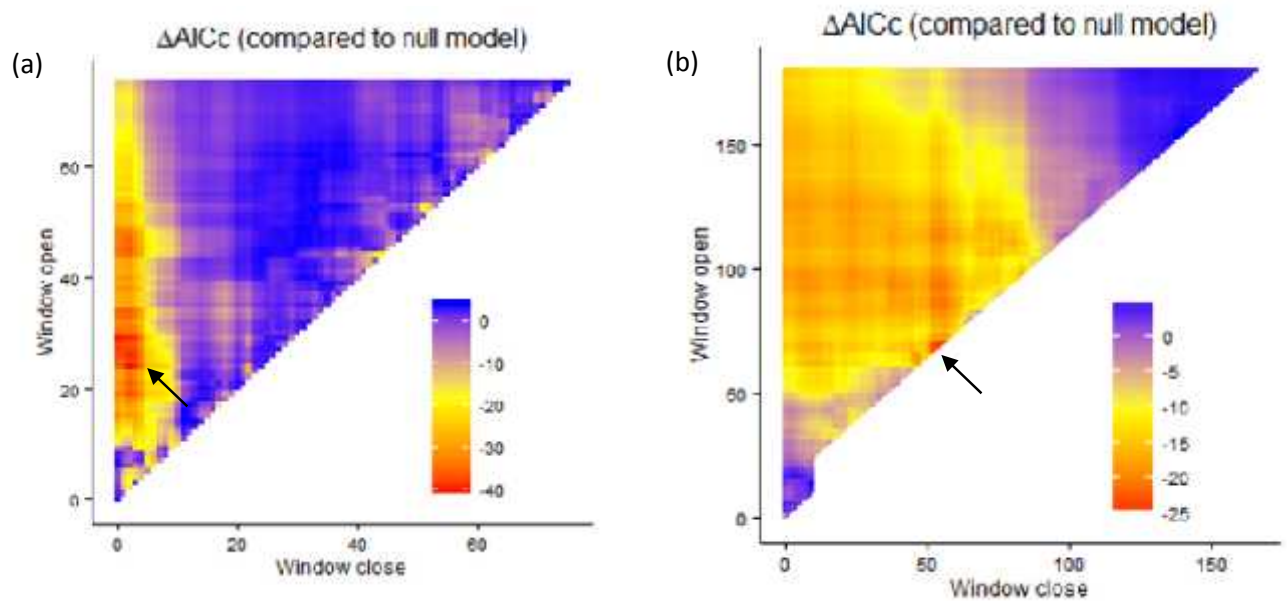


Figure 3. (a) Clutch size and (b) number of recruits (fledglings that survived 6 weeks after fledging), increased with the amount of rainfall in the month prior to egg-laying. Dashed line show regression line through the intercept. Results from generalized linear mixed models with Poisson distribution. Boxplots' width adjusted to sample size showing the interquartile range (box), medians, SE and dots show outliers, n = number of nests

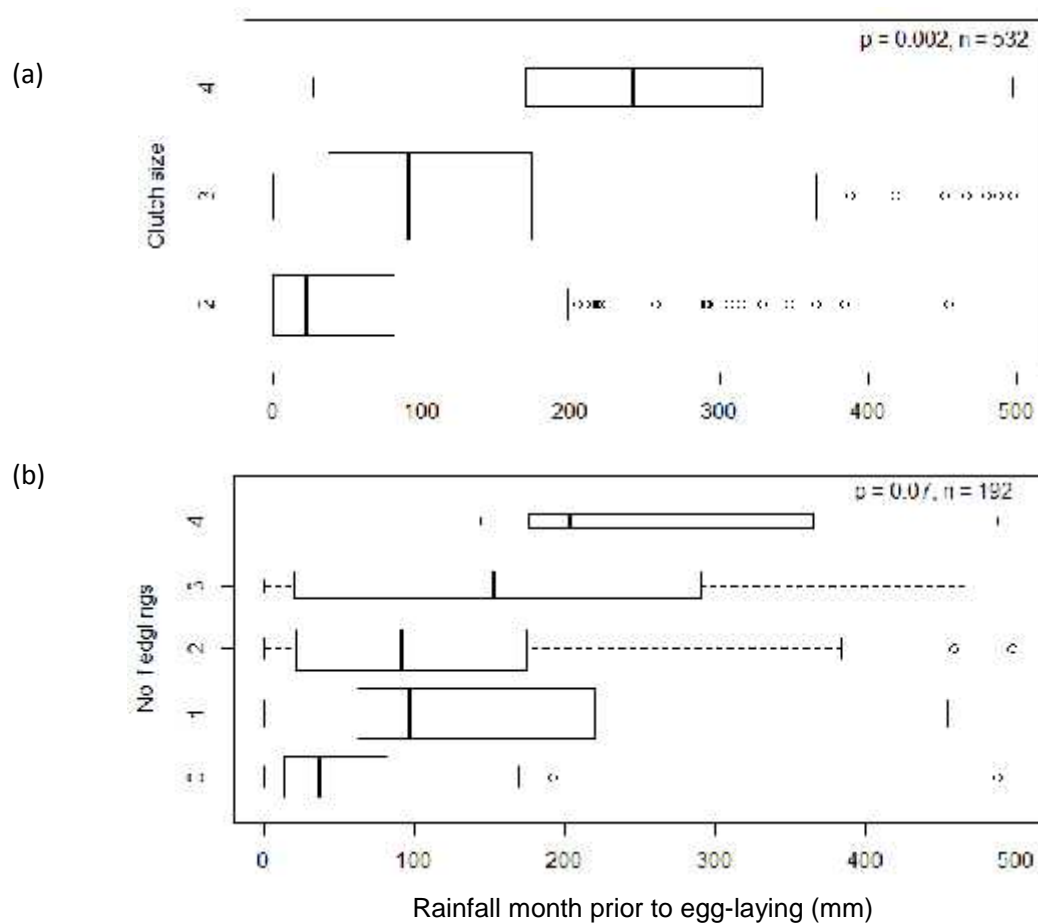


Figure 4. Monthly arthropod abundance (average of summed length of all arthropods) correlates with the number of recruits (number of fledglings that survived to 6 weeks after fledging) at the population level. Data from September 2007 until June 2010. Dashed line show regression line through the intercept. Results from a Spearman correlation.

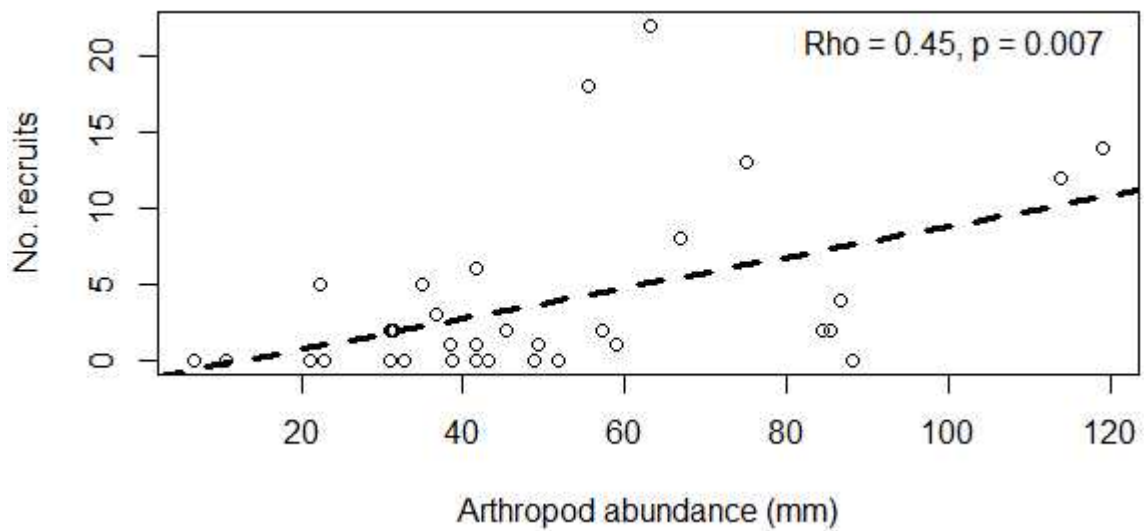
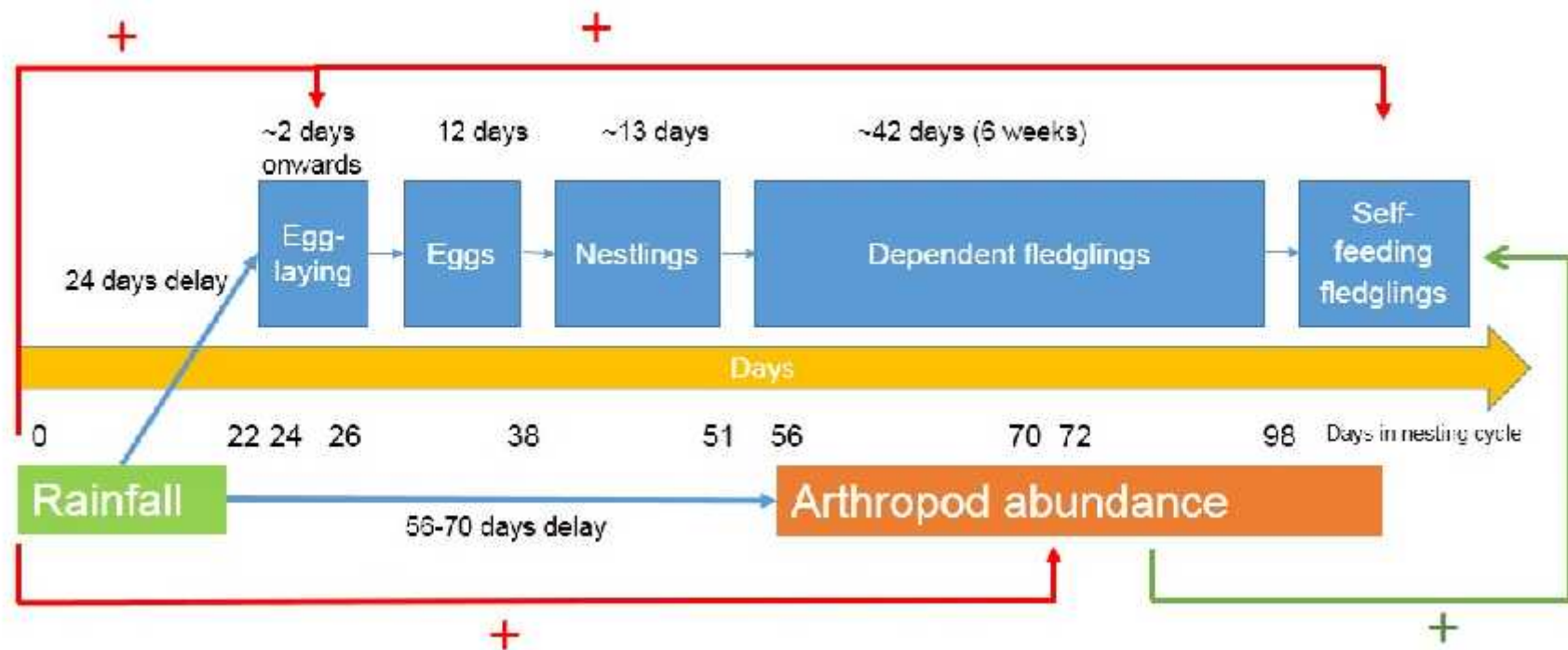


Figure 5. Schematic representation of timing of rainfall in relation to nesting initiation and arthropod abundance. Red arrows represent the positive effect of cumulative rainfall during the critical climate window on clutch size, number of fledglings surviving to 6 weeks (recruits) and arthropod abundance, the green arrow indicates the direct positive effect of arthropod abundance on recruitment.



Supplementary Material

Table S1. Identifying the strongest critical climatic time window that affects (a) nesting and (b) resource phenology (arthropod abundance). Shown five best models for the effects of cumulative rainfall (cm) ordered by AICc with most negative values first. AICc is computed against the null model on no climate effects. The quadratic effect of rainfall was the best supported signal for both nesting and resource phenology. Information from all fitted climate windows (days before event). Window type is “relative”, range time period is: 0-75 days for nesting and 0-180 days for arthropod abundance*

(a)						
Nesting	AICc	Window opens	Window closes	SE		
	-40.28	24	2	0.20	0.03	0.08
	-40.14	29	0	0.17	0.02	0.07
	-39.65	24	3	0.20	0.04	0.06
	-39.47	29	1	0.18	0.03	0.05
	-39.38	29	2	0.20	0.03	0.05

(b)						
Insect abundance	AICc	Window opens	Window closes	SE		
	-25.57	70	56	0.54	0.18	0.01
	-24.55	70	54	0.47	0.18	0.007
	-24.53	70	55	0.48	0.19	0.007
	-24.51	68	54	0.52	0.18	0.007
	-24.31	70	53	0.44	0.18	0.007

*for further details on the model structure refer to Bailey & van de Pol (2015), van de Pol & Cockburn 2011 and van de Pol et al. (2016)

Figure S1. Seasonality of nesting, climatic variables and arthropod abundance. (A) Monthly means of daily maximum and minimum temperature for records from Fitzroy Crossing (003093, ~95Km south West), mean \pm SE for Jun2006 to Nov2010. (B) Percentage of territories with breeding activity (initiating nests and/or until fledglings are present for 3 weeks), mean \pm SE for Jul2006 to Nov2010. (C) Mean monthly rainfall, mean \pm SE for rainfall data at Mornington Wildlife Sanctuary from Jun2006 to Nov2010. (D) Monthly arthropod abundance represented by total length of all arthropods captured per sweep in mm, mean \pm SE for Sep2007 to Jun2010

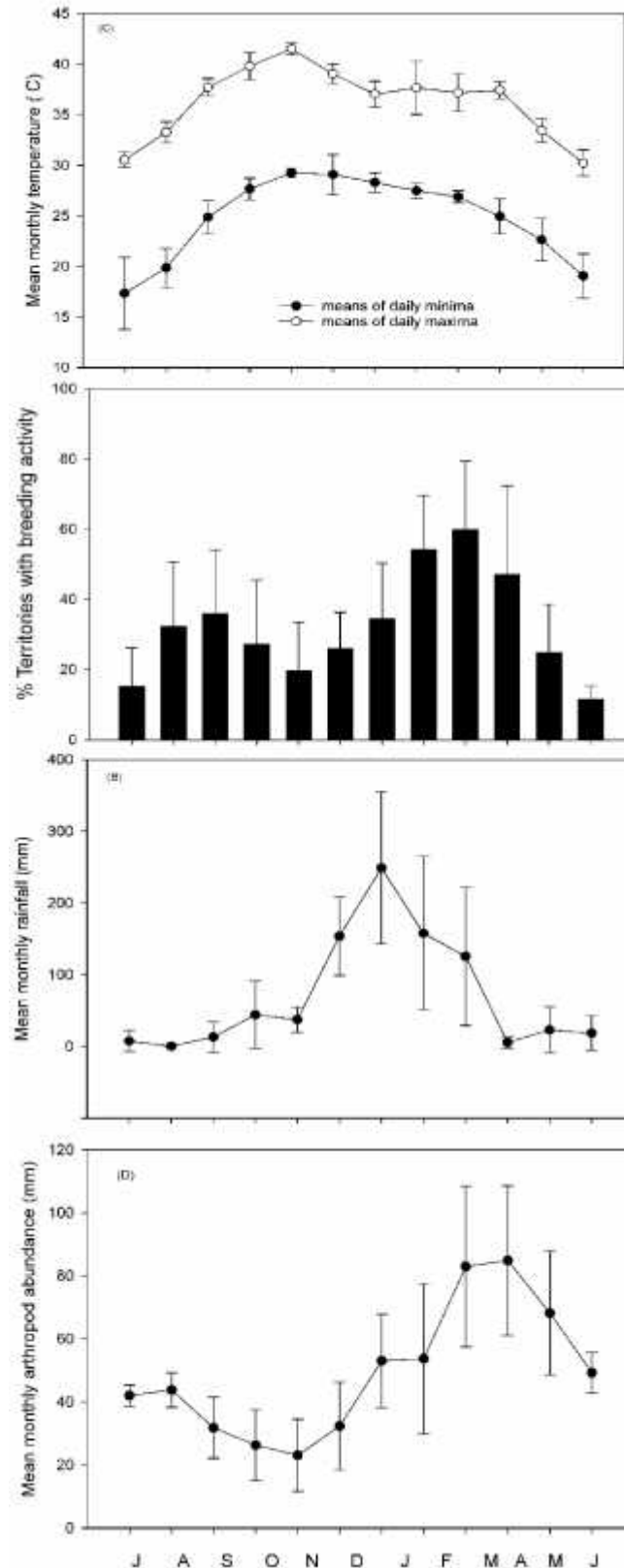


Figure S2. Model support for all fitted time windows tried for (Δ AICc) temperature in relation to (a) nesting initiation and (b) arthropod abundance. Panel showing window open (y-axis) and window close (x-axis) in which models with the lowest Δ AICc (red) are the best supported. Notice lack of window for temperature which has been further confirmed with randomization of the data. The patterns evident in panel b indicate the seasonal variation in temperature (notice scale ~300 days). Strongly supported windows are grouped together. For further information refer to van de Pol et al. (2016).

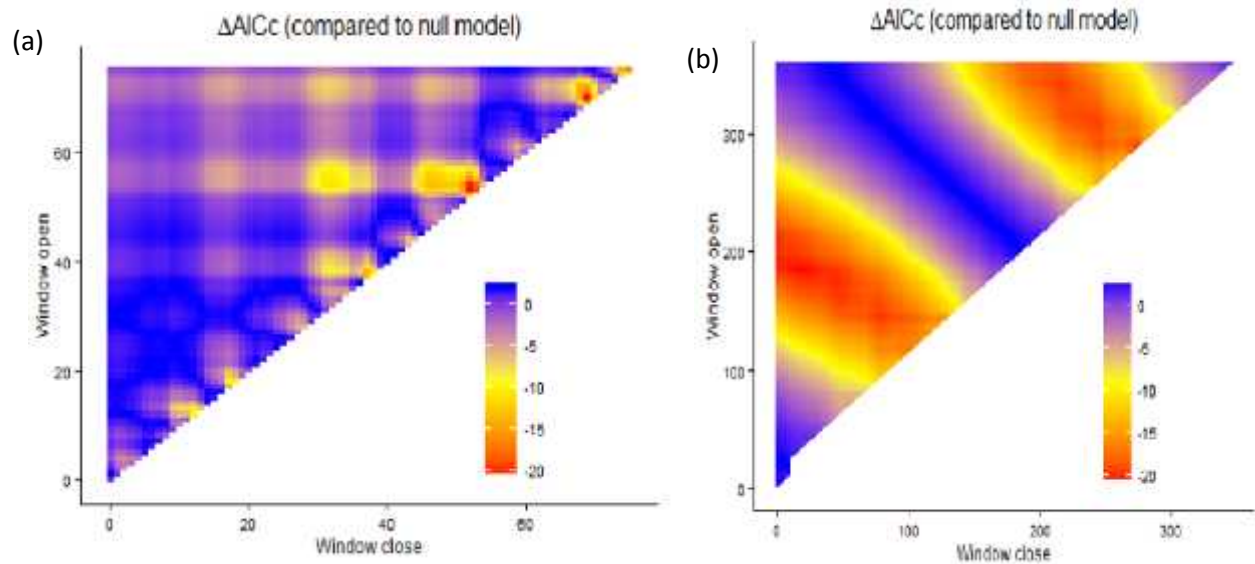
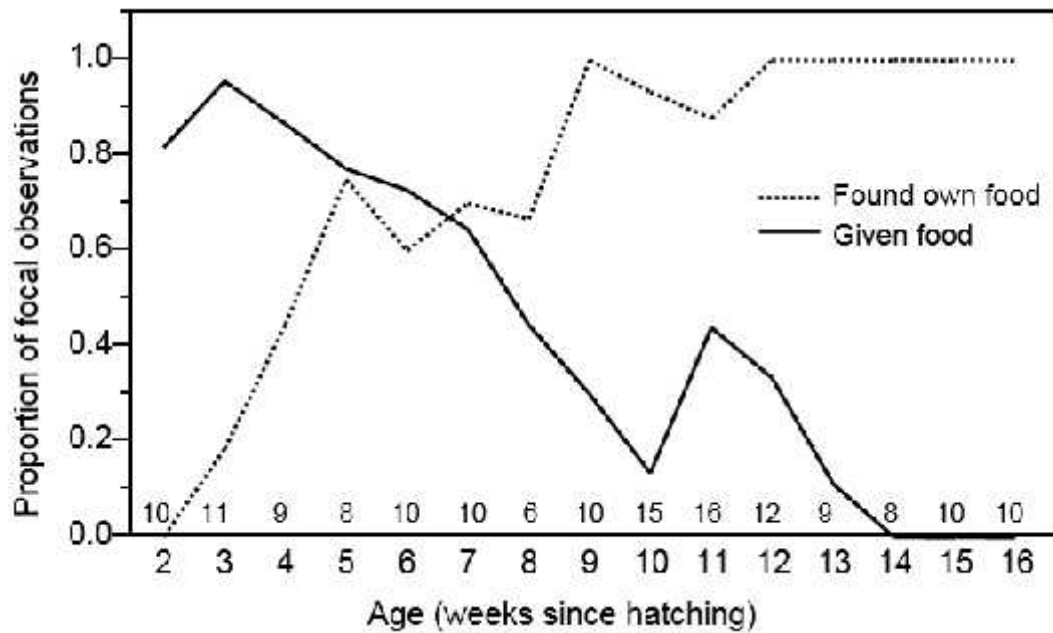


Figure S3. Proportion of focal watches when fledglings were fed (black line) or when they found their own food (dotted line). The number of fledglings observed in each age category is shown at the bottom of the graph.



Declaration for Thesis Chapter 2

Declaration by candidate

In the case of Chapter 2, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The key ideas, data collection, data analysis, lab work and writing of the manuscript were my responsibility.	90

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution
Anne Peters	Assistance with writing manuscripts, design of hypotheses, data collection, interpretation of results, feedback on thesis
Michelle L. Hall	Assistance with writing, data collection, interpretation of results.
Sjouke A. Kingma	Assistance with writing, data collection, interpretation of results.
Kaspar Delhey	Assistance with writing, data analysis, interpretation of results.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work.

Candidate's Signature

Date: 15-10-2016

Main Supervisor's Signature

Date: 15-10-2016

Chapter 2

Contrasting effects of climate means and extremes on nest failure and productivity in an endangered tropical bird

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**This chapter has been submitted to Functional Ecology*

Abstract

Determining effects of climate on reproduction is vital to predict population dynamics and extinction risks under future climate scenarios. Such studies are especially needed for tropical species given their susceptibility to environmental change and limited available information. We studied fine-scale effects of habitat quality and climate means and extremes on nest success over 5 years (685 nests) in a resident bird of the monsoonal tropics (*Malurus coronatus*). High average rainfall increased the likelihood of nest flooding, responsible for losses of 15% of nests. Nest flooding was less likely in higher-quality habitats (i.e. with more vegetation cover). Individual adaptive responses, increases in nest height following flooding, were only partly successful, possibly because nest predation risk favored lower nest height. Predation caused 57% of nest losses, and was less likely in higher-quality habitat. Predation increased with increasing mean temperature, but decreased when temperatures were extremely high, presumably due to temperature-related variation in reptilian predator activity.

Overall, nest failure rates were higher with higher average temperature and rainfall and in lower quality habitat. For successful nests, extremely hot temperatures reduced hatching success and high average rainfall reduced fledgling survival. Taken together, these results suggest that ongoing warming, increased rainfall and habitat degradation are likely to reduce reproductive success in this endangered bird. Such processes are likely to be important across similar tropical regions.

Key words: heatwave, global warming, precipitation, temperature extremes, climate change, tropical

Introduction

Global climate change and habitat degradation have been identified as increasing threats to biodiversity (Foden et al. 2013, IPCC 2013, Maxwell et al. 2016). Forecasting these effects on species' reproduction has become an urgent priority to generate relevant information for the future management of sensitive species (Foden et al. 2013). To date, most studies have focused on climatic changes in temperate regions (Møller et al. 2010, Pacifici et al. 2015). However, most of the world's biodiversity is concentrated at tropical latitudes and little is known about how tropical species (will) respond to such changes (Charmantier and Gienapp 2014). Moreover, theoretical models and recent evidence suggest that tropical species are more vulnerable to the effects of climate change than previously assumed (reviewed in ekerccio lu et al. 2012).

Although the pervasive nature of global climate change is now widely recognized, the majority of studies on the ecological impacts of climate change have focused on average temperatures, and effects of changes in average precipitation are still poorly understood (Easterling et al. 2000, Lehmann et al. 2015). Moreover, extreme climatic events are becoming more frequent globally, with increasing record-breaking high temperatures (IPCC

2013) and extreme rainfall events (Lehmann et al. 2015) in the last three decades. Such trends are particularly important for tropical areas, since temperatures are already high, and their seasonal patterns strongly defined by rainfall (IPCC 2013). Responses to different components of the same climatic variable (i.e. means versus extremes) do not necessarily occur in the same direction and should be therefore considered in conjunction (Bailey and van de Pol 2016).

Reproduction is a critical part of any life cycle, and understanding the differential impact of means and extremes of climate on different stages of reproduction is central to understand how climate affects the fitness of organisms, and ultimately their population dynamics (Senapathi et al. 2011, Pacifici et al. 2015). For example, in birds - one of the most studied taxa in relation to global change – total nest failure might be caused by extreme climatic events (e.g. heat waves, droughts, flooding, fires) affecting productivity at the population level (Grant et al. 2000, ekericio lu et al. 2012). Furthermore, birds could be affected at a finer-scale: embryo development can be impaired at extreme temperatures (Stoleson and Beissinger 1999), nestling survival and development affected by increasing mean and extreme temperatures and precipitation (Senapathi et al. 2011, Cunningham et al. 2013) and adults can alter their parental care (e.g. disrupting nest attendance or chick provisioning) (Grant et al. 2000, du Plessis et al. 2012). This highlights the importance of identifying biologically relevant thresholds of climate that potentially affect the likelihood of success, development and survival of offspring. At the same time, the effects of climatic means and extremes might be attenuated or exacerbated according to the quality of the habitat in which individuals are found (ekericio lu et al. 2012). Thus, quantifying habitat quality (e.g. vegetation cover) and variation in climate simultaneously is essential to understand how all effects combine and affect the final outcome of reproduction, therefore generating relevant information for management of species (ekericio lu et al. 2012).

Here we investigate the effects of variation in means and extremes of rainfall and temperature on nest success of a tropical resident bird, the cooperatively breeding purple-crowned fairy-wren (*Malurus coronatus coronatus*). This endangered bird is endemic of north-west Australia, with distinctly seasonal but highly variable rainfall and high temperatures typical of the monsoonal tropics (Hughes 2003, Moise et al. 2015). Using five years of detailed nest monitoring, we analyze the effects of climate and habitat quality on the causes of total nest failure, and on several stages of reproduction (incubation, hatching-, fledging- and post-fledging success) and total productivity of nest attempts.

Methods

Study site and population

A population of purple-crowned fairy-wrens was monitored at Mornington Wildlife Sanctuary- managed by Australian Wildlife Conservancy and located in northwest Australia (17°31' S, 126°6' E) along ~15 km of river along Annie Creek and the Adcock River (Kingma et al. 2009). At this site, purple-crowned fairy-wren territories occur exclusively in riparian vegetation containing the palm-like *Pandanus aquaticus*. Habitat quality; density, width and height of *Pandanus* stands, varies throughout the study site. The study area is located in the monsoonal tropics, with a prominent wet season during December – March. All birds in our study population (n = 125 in 2005 increasing to 151 in 2010) were individually color banded and monitored throughout their life. Each territory is defended by a dominant pair (Hall and Peters 2008), sometimes accompanied by subordinates (range 2-8 subordinates) which are mostly (~60%) offspring of the dominant pair. Only the dominant pair reproduces, and subordinates participate in offspring care, improving reproductive success and breeder survival (Kingma et al. 2009, 2010). Although breeding can occur in

every month of the year, there is a clear peak during and after the wet season (Dec-Mar) and sometimes a small peak during the dry season (Sep-Oct) (Peters et al. 2013).

Nest monitoring

Between July 2006 and November 2010, we recorded 685 nesting attempts (details in Table S1). Nests are open cup and built exclusively by the breeding female (details in Chapter 1). For each nest, nest location, height above ground level and location coordinates were recorded. By far the majority of nests (96%) were built in *Pandanus*, on average 1.5 ± 0.05 m above the ground (range 0.15-6.50 m, $n = 658$). Laying date and clutch size (1-4 eggs) were determined by checking nest contents at three-day intervals after building was complete. Eggs hatch 13 days after the last egg is laid. Nestlings were banded on day 7 with a combination of colored leg bands and a numbered band supplied by the Australian Bird and Bat Banding Scheme. Nestlings usually leave the nest 12 or 13 days after hatching ($n=16$ nests; unpubl. data) and the territory area was monitored weekly to locate fledglings and determine their survival. Fledglings are fed by group members until approximately 13 weeks of age (11 weeks post-fledge), but frequently find their own food from 9 weeks of age; 90% of fledglings that reach 9 weeks survive until adulthood (unpubl. data). Nests were considered to have been depredated if a nest known to have contained eggs and/or nestlings was found empty, often with clear signs of predation (i.e. damaged, predator seen attacking the nest, or identifiable scats found inside).

Environmental variables

Rainfall and temperature. Daily rainfall records were obtained from a weather station at Mornington Wildlife Sanctuary since 2005 (Australian Bureau of Meteorology (BoM) weather station 002076, Fig.S1). On average, rain fell on 68 days per year, with daily

rainfalls averaging 12 mm (based on $n = 285$ days with rain from 2005-2010) and extremes > 48.4 mm (95th quantile from data 2005-2010). Daily temperature records for Mornington were only available from January 2008-July 2010, so we used temperature data from Fitzroy Crossing, which had records for our entire study period (BoM weather station 003093, 18.19°S, 125.56 °E, ~ 95 km SW from our study area, Fig. S1), and that is strongly correlated with data from Mornington Sanctuary (Spearman $Rho = 0.94$, $P < 0.001$, $n = 30$ months). The average daily maximum temperature was 36.2°C (62% of days during our study period reached temperatures $> 35^\circ\text{C}$) and extremes were $> 42.5^\circ\text{C}$ (95th quantile) and $> 40^\circ\text{C}$ (90th quantile from data 2005-2010).

Territory quality. Purple-crowned fairy-wrens in this region do not occupy habitat without *Pandanus* and they depend strongly on this vegetation (Kingma et al. 2011a). *Pandanus* cover varies widely between territories, and territories with greater *Pandanus* cover have more subordinates (Kingma et al. 2011b), indicating that these territories are more productive or attractive for subordinates. Moreover, dominant females target territories with greater *Pandanus* cover during breeder dispersal (i.e. divorce, Hidalgo Aranzamendi et al. 2016). Therefore we used total *Pandanus* cover as an index of territory habitat quality (ranging from 1-20, as in Hidalgo Aranzamendi et al. 2016). Group size was also considered as a component of territory quality because subordinates increase breeder survival and fledgling recruitment (Kingma et al. 2010).

Statistical analyses

All analyses were done in R 3.2.0 (R Core Team 2015). We followed a mixed modelling approach with model selection based on AIC coefficients. Interactions between habitat quality and climate variables were included in the original models; these were all removed

since they were not statistically significant (data not shown). Samples sizes vary for each analysis due to missing data, and are shown in tables.

Total nest failure. A nest was classified as successful if it resulted in at least one fledgling. A generalized linear mixed model (GLMM) with binomial distribution was built to assess factors affecting nest success ignoring the cause of failure (successful=1, unsuccessful=0). Here, 16 nests that experienced partial predation and were eventually abandoned were coded as unsuccessful. Additionally, we separately investigated factors affecting nest flooding and nest predation, the dominant sources of nest failure (included only fledged and flooded or depredated nests respectively). As explanatory variables we included climatic variables compiled for the duration of the reproductive attempt: average temperature, exposure to extreme temperature, average daily rainfall and exposure to extreme rainfall. Since the duration of nest survival correlates with the number of days a nest is exposed, exposure to extreme temperature/rainfall was coded as a binomial variable (experienced at least one extreme day = 1, none = 0). In the nest predation model, we used 40°C (90th quantile) as a threshold for extreme temperatures, because temperatures > 40°C reduce the foraging activity of monitor lizards in the monsoonal tropics (Greer 1989) and these are main known predators of riparian species in this area including purple-crowned fairy-wrens (Doody et al. 2015, for details see results). Month was included as a continuous linear and quadratic variable (month 1= July), to control for temporal variation in nest success. Average temperature and month as a quadratic term were highly correlated ($r > 0.71$), as well as average daily rainfall and extreme rainfall ($r > 0.82$). Therefore, four models were built using each variable at a time, here we present the model with the lowest AIC coefficient (see Supplementary Material for results of alternative models and further details on model selection). Other environmental variables included were: habitat quality (*Pandanus* cover), group size, and nest height.

Components of nest success. For nests that did not fail completely (i.e. hatched or fledged at least one young respectively), we tested if environmental variables affected hatching success (proportion of eggs that hatch), fledging success (proportion of chicks that fledge) and post-fledging success (proportion of fledglings that survived until week 9). In each model, we included the climate experienced during each stage for each nest (from egg-laying to hatching (nests = 208), from hatching to fledging (nests = 168) and 6 weeks from fledging (nests = 168)). We built glmmPQL models, since they were the best fit to our data, using the *cbind* command with (number of surviving, number not surviving) as response variables and the environmental variables detailed above as independent variables. Models of nest failure performed better (lower AIC) using average daily rainfall (Table S2) and here we only tested for average daily rainfall. Total productivity of a nest attempt was defined as the number of fledglings that survived until 6 weeks after fledgling (~9 weeks old). We tested if the number of fledglings from successful (not depredated, not flooded, not abandoned) nests (Poisson distribution, 0-4) was affected by climatic and environmental parameters experienced during the total nest cycle (i.e. from egg-laying until fledglings survived 9 weeks) using a GLMM. Nests with a value 0 produced at least one fledgling but none survived to week 9.

Results

Factors affecting total nest failure

The majority of breeding attempts failed (77% of 685 nests did not produce a single fledgling). Nest inundation (flooding) caused 15% of nests to fail (Fig. 1). Low nest height increased the likelihood of nest flooding, as did high average rainfall (mean flooded nests = 44.3 mm/day, non-flooded nest = 18.8 mm/day, Table 1a, Fig. 2). Although extreme rainfall and average rainfall predicted nest failure in the same direction, average rainfall was clearly a

better predictor of nest flooding (Table 1a, Table S2). On average, females that lost a nest due to flooding built the subsequent nest in a higher site ($n = 77$, paired $t = -2.08$, mean flooded nests = 1.38 m, mean re-nest after flooding = 1.71 m, $p = 0.04$; Fig. 2), but 30% of these subsequent attempts were also lost to flooding. Overall, successfully fledged nests were located higher than nests lost to flooding ($n = 360$ nests, $t = 2.54$, mean flooded nests = 1.35 m, mean fledged nests = 1.68 m, $p = 0.01$).

Nest predation was the main cause of nest failure (57% of nests; Fig. 1, Table S1). Most depredated nests were found torn apart. Direct observations and camera trap recordings of predation events identified reptiles as the primary predators (details in Table S1). Nests were less likely to be depredated during periods of lower average temperatures and extreme rainfall (Table 1b, Fig. 1; average rainfall did not appear to have an effect, Table S1).

Predation was also lower when nests experienced temperatures above 40 °C, and in territories with higher habitat quality (Table 1b). Higher-placed nests were more likely to be predated (Table 1b, Fig. 2), although this effect was less strong than the opposite effect for flooding (Table 1a, Fig. 2). Females that lost a nest due to predation built a subsequent nest at a lower position, although the difference was not very large and not statistically significant ($n = 146$, paired $t = 1.38$, mean depredated nests = 1.66 m, mean re-nest after predation = 1.49 m, $p = 0.16$; Fig. 2).

Overall, nests were more likely to be successful (i.e. fledge at least one young) when the average temperature they experienced was lower, when they received less rain on average, and when located in territories with higher quality habitat (greater *Pandanus* cover) (Table 1c).

Factors affecting hatching and fledging success

Overall, 23% of clutches produced at least one fledgling (i.e. escaped total nest failure, Table S1). Hatching success (mean = 0.89 ± 0.24 SE of eggs hatched when total nest failure was excluded) was greater at higher average temperatures but lower if a nest experienced extreme temperatures above 42.5°C (Table 2a, Table S2 for results of alternative models, Fig. 1). No climatic variable affected the proportion of hatchlings that fledged (mean = 0.83 ± 0.26 SE of hatched eggs fledged, excluding total nest failure) (Table 2b, Fig. 1), but larger groups tended to have higher fledging success (Table 2b). The proportion of fledglings that survived 6 weeks after fledging (mean = 0.65) was lower when rainfall was higher (Table 2c, Fig.1). Over the entire nest cycle, no climatic variable influenced the number of surviving fledglings produced per successful nest (mean = 1.3 ± 1.0 SE fledglings per nest were recruited from breeding attempts that did not completely fail). The only marginally significant effect was that larger groups tended to have higher recruitment per nest (absolute number of chicks, Table 2d).

Discussion

Understanding the effects of climate variation on the reproductive cycle of animals has become a research priority in view of the rapid changes in global climate (Senapathi et al. 2011). To date, such effects have been poorly studied in tropical species (Grant et al. 2000, Senapathi et al. 2011). Here, we reveal the intricate effects of environmental variation on different aspects of reproduction in a tropical bird, where nesting success varies as a function of the direction of the effects exerted by climatic means and extremes (Fig.1).

Rainfall. Rainfall affected nest failure in two ways, high average rainfall increased the chance of flooding (Fig. 1), and at the same time extreme levels of rainfall reduced the risk of predation (Fig. 1). Reduction of nest predation rates due to rainfall have been recorded for

several bird species from temperate and tropical regions (Morrison and Bolger 2002, Oppel et al. 2013, Ancil et al. 2014), possibly due to the effects on abundance and activity levels of most reptilian and avian predators (White 2008, Doody et al. 2015). Surprisingly for a bird that has peak reproduction during the wet season, and despite the larger effect of nest predation on nest failure, the overall effect of rain on nest survival was negative (Table 1c). Additionally, high average rainfall reduced fledgling survival for successful nests (Fig. 1). Since fledglings completely depend on adults for food (Kingma et al. 2010), rainfall interfering with provisioning by group members is a likely explanation for a decline in offspring survival (Grant et al. 2000, Ancil et al. 2014, Öberg et al. 2015).

Phenotypically plastic individual responses could mitigate effects of climate change (van de Pol et al. 2010). Indeed, we found evidence of plastic, adaptive nest site selection in response to flooding, albeit with limited success. Higher-placed nests were more successful in general, and following nest loss due to flooding, females built the subsequent nest in a higher location (Fig. 2). However, a third of those attempts were lost again to floods. Furthermore, predation risk favors lower nest heights (Table 1b, Fig. 2, lower height is associated with reduced predation risk), potentially limiting adaptive increases in nest height. Indeed, predation and flooding seem to be antagonistic forces upon individual responses on nest site selection.

It is unclear how the overall negative effect of high average rainfall on nest success, both at the level of likelihood of total nest failure and productivity of successful nests, will work out in the future. This is mainly because current climate model predictions for expected changes in average rainfall for the monsoonal tropics have low confidence, although all models and our long-term data (Fig. S3) show no tendency to increase, thus there appears no imminent threat (Moise et al. 2015). In contrast, there is high confidence that extreme rainfall events for the tropics and monsoonal Australia are increasing (Lehmann et al. 2015, Moise et al. 2015, Fig. S3). Although this might result in lower nest failure rates due to predation, it seems more

probable that flooding will become more frequent, as it has been recorded for the past three decades at our study site (Fig. S2).

Temperature. Variation in temperature also had pervasive effects on reproductive success. Nest predation probability changed with temperature, with evidence for antagonistic effects: increasing average temperature increased predation, but very high temperatures (at least one day $> 40^{\circ}\text{C}$) decreased it (Table 1b, Fig. 1). This pattern matches the optimal foraging temperature range of reptilian predators, particularly monitor lizards. These are the main nest predators of riparian bird species in monsoonal Australia, and their activity increases as it becomes warmer but it stops when temperatures exceed 40°C (Greer 1989, Doody et al. 2015).

Temperature extremes affected viability of eggs: hatching success was reduced after exposure to at least one day of extreme temperatures ($> 42.5^{\circ}\text{C}$, Table 2a, Fig. 1). Passerine embryos optimally develop between $36\text{--}40^{\circ}\text{C}$ and temperatures above 42.5°C arrest development and are considered lethal (Stoleson and Beissinger 1999). It appears that females are not fully capable of compensating for extreme temperatures, and eggs presumably became warmer than optimal, resulting in hatching failure.

In view of the ongoing increase in average temperature and frequency of heat-waves, worldwide (IPCC 2013) and in Australia (Moise et al. 2015), including our study site (Fig. S4), several predictions of their impacts on purple-crowned fairy-wrens can be made. Our data suggests that predation levels will increase with increasing milder temperatures, but this could be offset by predation rate decrease due to the increase in days over 40°C . However, once days with temperature $> 42.5^{\circ}\text{C}$ become common, viability of eggs will be at risk. Ultimately, the net effect of temperature changes over time will thus depend on the nature of the changes in the temperature distribution, hampering straightforward predictions of climate

change impacts, and this could be similar in other birds of similar ecology and size (McKeechnie et al. 2012).

Habitat. The positive effects of habitat quality (*Pandanus* cover at the territory level) were pervasive, including a lower likelihood of flooding (Table 1a, Fig. 1) and lower risk of predation (Table 1b, Fig. 1), which translated into higher nest survival in better quality habitat (Table 1c, Fig. 1). The reduced risk of flooding is presumably a result of larger, denser stands of *Pandanus* offering nest opportunities higher up the bank, and the lower predation risk probably results from a greater variety of nest sites offering concealment against predators (Soanes et al. 2015). Although there were no buffering effects of habitat quality on climatic effects (as indicated by the lack of significant interactions between climatic variables and habitat quality), and although habitat quality did not affect fledging success and fledgling survival, the direct and strong effect of habitat quality on nest success indicates that habitat preservation is critical for this species, as with many other species (Cokercioğlu et al. 2012, Öberg et al. 2015).

Conclusions. Our results highlight the variety of effects that climate can have on nesting success. Some of the effects of means and extremes were opposite (e.g. temperature – predation), some effects were direct (rain – flooding, temperature – hatching success) and some indirect (via predator activity or bird behavior), and most effects varied with the stage of the nesting cycle. Our analysis showed not only that the effect of climate is better understood when analyzed stage by stage, but also that these varied, opposing effects might hamper species adaptive responses (e.g. nest height). This complexity, potentially inherent to other tropical systems with high climate variability (Rubenstein et al. 2016), highlights the challenge of predicting the effects of long-term climatic change on such populations. This is particularly relevant since most climate studies have focused on temperate populations and

temperature-related consequences (Charmantier and Gienapp 2013). Our understanding of the potential effects of climate change on the life history of tropical species is still incomplete, which limits the scope of our forecasts and complicates formulation of ameliorating strategies.

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Table 1. Climatic and environmental factors that affect the probability of nest failure in purple-crowned fairy-wrens. Results of GLMMs with binomial responses using (a) probability of nest not flooding (b) probability of nest not succumbing to predation and (c) overall probability of nest not completely failing (producing at least one fledgling)^a. Random factor (pair identity) did not contribute to variance of the models (data not shown). Shown are model estimates (continuous variables are scaled), their standard error (s.e.), t value and significance (p). Results $p < 0.05$ shown in bold.

	(a) probability of nest flooding (success = 1)				(b) probability of nest predation (success = 1)				(c) overall probability of nest failure (success = 1)			
No. nests (pairs)	234 (114)				381(141)				501(157)			
Parameter	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p
Intercept	-3.02	0.94	-3.22	0.001	-2.11	0.41	-5.16	<0.001	-2.52	0.39	-6.37	<0.001
Nest height (m)	0.9	0.31	2.93	<0.01	-0.22	0.12	-1.85	0.06	-0.08	0.11	-0.73	0.47
Extreme temperatures (y/n) ^b	0.52	0.98	0.53	0.6	0.94	0.3	3.12	<0.01	0.52	0.35	1.47	0.14
Average temperature (°C) ^c	-0.43	0.19	-2.34	0.02	-0.18	0.05	-3.67	<0.001	-0.09	0.04	-2.08	0.04
Extreme rainfall (y/n) ^b	n.a.	n.a.	n.a.	n.a.	0.82	0.41	1.99	0.05	n.a.	n.a.	n.a.	n.a.
Average rainfall (mm) ^c	-0.62	0.11	-5.82	<0.001	n.a.	n.a.	n.a.	n.a.	-0.14	0.03	-4.07	<0.001
Month (linear) ^d	-0.28	0.22	-1.31	0.19	0.13	0.04	3.07	<0.01	0.08	0.04	1.96	0.05
Habitat quality ^e	0.24	0.06	4.23	<0.001	0.06	0.02	2.64	<0.01	0.09	0.02	3.65	<0.001
Group size ^f	0.1	0.19	0.55	0.58	0.13	0.09	1.52	0.13	0.11	0.09	1.27	0.21

^a a nest was classified as successful if at least one fledgling was recorded, success = 1, ^b coded as a factor (yes= experienced at least one day above threshold, estimate shown relative to yes), for temperature days > 42.5°C for nest success model and > 40°C for nest predation model, for extreme rainfall threshold > 48.4 mm, ^c climate recorded during the lifetime of a nest from egg-laying until fledging or nest failure, ^d month (1 = July) in which the nest was initiated, ^e habitat quality refers to *Pandanus* cover, ^fgroup size is number of subordinates and adult birds. n.a. = term not fitted in the models

Table 2. Climatic and environmental factors that affect the different components of nest success in purple-crowned fairy-wrens. Dataset includes first and re-nesting attempts, excludes nests that were completely unsuccessful. Random factor (pair identity) did not contribute to variance of the models. (a-c) Results of glmmPQL using a proportion of no. birds hatched/fledged/survived 6 weeks after fledging from the total no. of eggs, total no. birds hatched, total no. birds fledged respectively. (d) Results of GLMM using number of fledglings as response variable. Shown model estimates (continuous variables are scaled), their standard error (s.e.), t value and significance (p). Results $p < 0.05$ shown in bold.

	(a) Hatching success ^a				(b) Fledging success ^a				(c) Post-fledging success ^a				(d) Total productivity of a successful nest ^b			
No. nests (pairs)	208 (109)				168 (97)				168 (97)				188 (109)			
Parameter	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p
Intercept	4.28	0.79	5.42	<0.01	0.10	0.54	0.18	0.86	0.46	0.50	0.93	0.36	0.11	0.22	0.50	0.62
Nest height (m)	0.12	0.18	0.73	0.47	0.03	0.15	0.16	0.87	n.a.	-	-	-	n.a.	-	-	-
Extreme temperatures (y/n) ^c	-0.82	0.41	-2.02	0.04	-0.26	0.46	-0.57	0.57	0.66	0.39	1.69	0.10	0.14	0.2	0.75	0.46
Average temperature (°C)	0.61	0.18	3.41	<0.01	-0.16	0.23	-0.73	0.47	-0.09	0.21	-0.41	0.68	0.09	0.09	0.97	0.33
Daily rainfall (mm)	0.3	0.17	1.75	0.08	0.17	0.17	0.30	0.30	-0.29	0.14	-1.95	0.05	0.03	0.09	0.35	0.73
Month (linear) ^d	-0.19	0.06	-3.28	<0.01	-0.01	0.06	-0.07	0.95	0.23	0.05	4.63	<0.01	0.35	0.08	4.25	<0.001
Habitat quality ^e	-0.07	0.06	-1.25	0.21	-0.02	0.03	-0.72	0.47	-0.01	0.03	-0.46	0.65	-0.02	0.01	-1.32	0.19
Group size ^f	-0.16	0.15	-1.08	0.28	0.21	0.11	1.85	0.06	0.11	0.11	0.99	0.32	0.09	0.05	1.83	0.07

^a climate recorded during each stage (e.g. from egg-laying to hatching, from hatching to fledging, from fledging until 6 weeks old), ^b Total productivity as number of fledglings that survived six weeks after fledging. Climate recorded since egg-laying until 6 weeks after fledging (total nest cycle), ^c days >42.5°C coded as a factor (yes= experienced at least one day above this temperature, estimate shown relative to yes), ^d month (1 = July) at start of nest, ^e habitat quality refers to *Pandanus* vegetation cover, ^f group size is number of subordinates and adult birds. n.a. = term not fitted in the model

Figure 1. Schematic representation of climatic and ecological effects on nest success. Sizes of boxes represent % of eggs with a particular fate (652 nesting attempts). Success rates are low (11%, green box); the main cause of failure is predation (57%), followed by flooding (15%). Problems during development (hatching failure, failure to fledge or recruit) make smaller contributions to overall failure rates. Orange arrows indicate negative effects on success and green positive effects. Overall failure is predicted to increase with increasing rainfall and with climate warming.

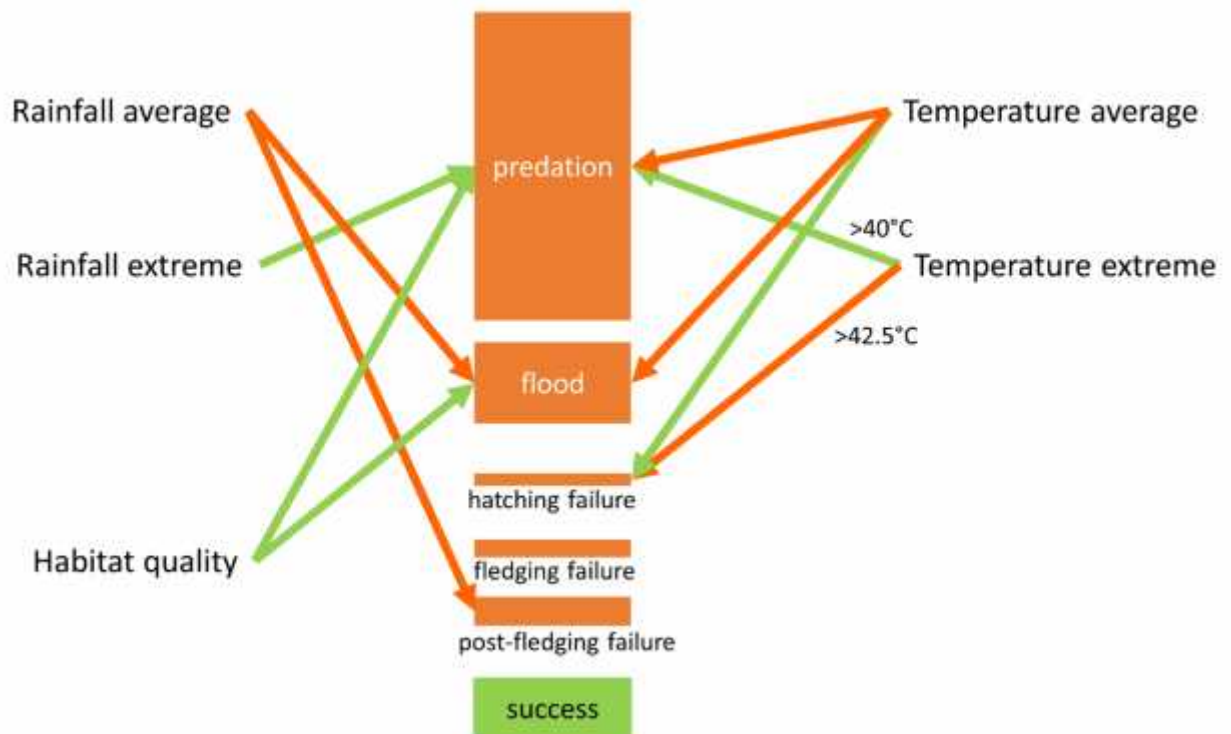
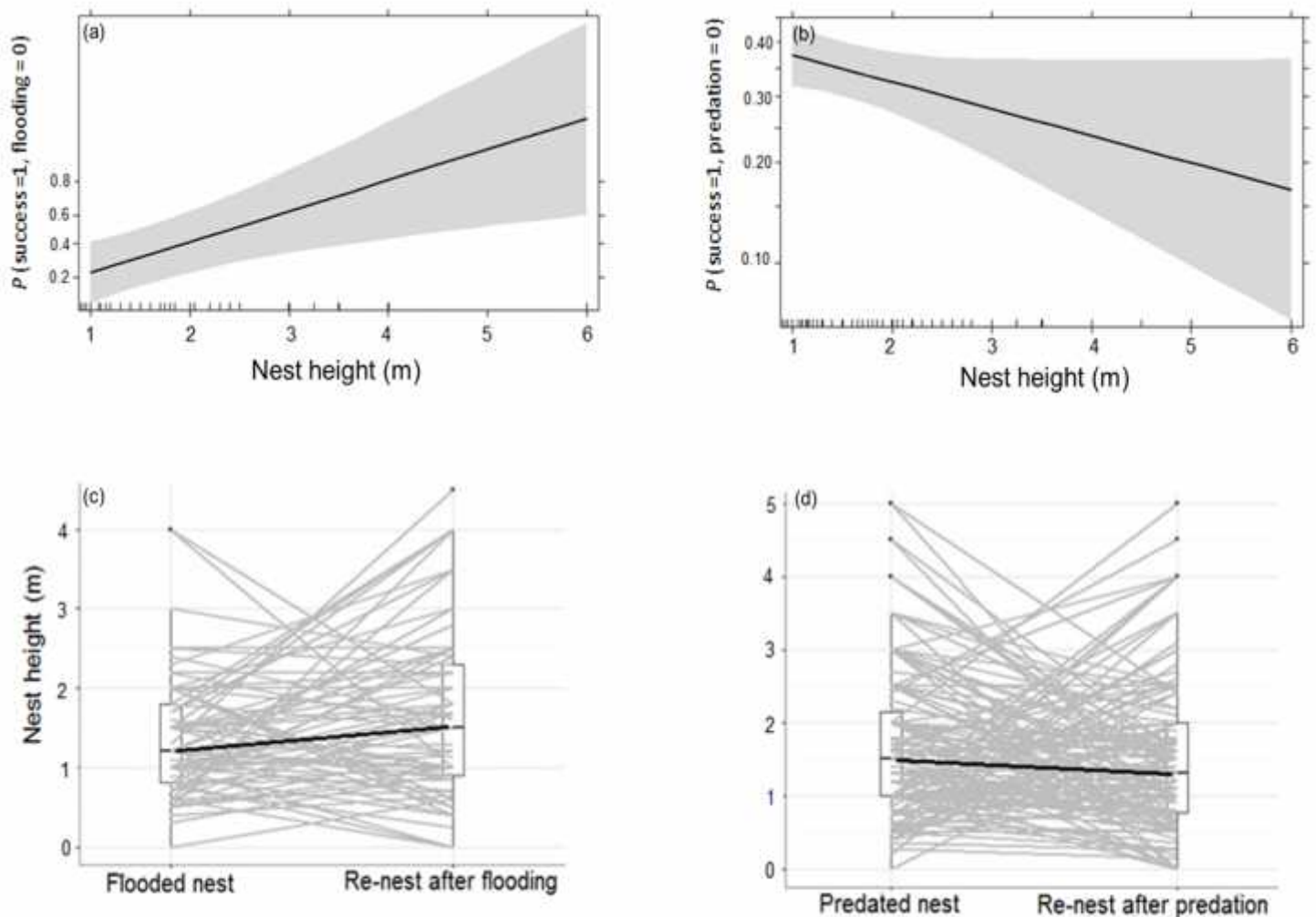


Figure 2. Adaptive phenotypic plasticity in nest height placement. Lower nest height (relative to substrate in meters) (a) increases risk of flooding but (b) reduces risk of predation (Table 1, nest success = 1). On average (c) subsequent nests after flooding were located at higher locations ($P = 0.04$) and (d) subsequent nests after predation tended to be at lower locations, although no significant difference was found ($P = 0.16$). Grey lines connect nesting attempts of the same individuals. Boxplots showing the interquartile range (box), medians (connected by bold horizontal line) and SE (error bars).



Supplementary material

Statistical analysis

Climate variables were fitted as linear and quadratic terms, and quadratic terms were removed if not statistically significant. Interactions between habitat quality and climate variables were included in the original model and then removed due to not being statistically significant. All combinations of explanatory variables that did not have strong correlations ($|r| < 0.7$) were included in the models. When two variables were highly correlated ($|r| > 0.7$), they were removed from the original model containing all variables and analysed in separate models using one of these variables at a time. Models containing month as a linear term performed better than those without it (based on AIC). Thus, we kept month as an explanatory variable to control for some unexplained temporal variation in success. Removing it from our models did not change the effect size or direction of variables significantly (results not shown). Models were first fitted using generalized linear models (GLM) without random terms to test for overdispersion. If data were not overdispersed, generalized linear mixed models (GLMM) were built with *lme4* (Bates et al. 2015) including pair identity as a random term. If data was overdispersed, we used GLMM with penalized quasi-likelihood (PQL) models, since such models fitted better our data, with the *MASS* package (Venables and Ripley 2002). Models were then ranked by AIC values using the package *MuMin* (Barton 2014). The models shown in results are the ones with the lowest value of AIC. These models were selected if they had more than 2 units of difference with the alternative model, which applied to all cases (Burham and Anderson 2002) (i.e. only one model selected to be the best one, outputs of alternative models found below). All continuous variables were scaled, centered and transformed if needed. Means (\bar{x}), estimates () and their standard error are presented (\pm SE).

Table S1. Outcomes of nesting attempts. The dataset includes numbers of first and re-nesting attempts. Four complete years are shown and 2010 is an incomplete year with estimates from July to November only*.

Nest outcome (numbers)	2006/7	2007/8	2008/9	2009/10	2010*	Totals
Failed prior to laying						
Unknown (predated or abandoned)	18	39	22	37	24	
Flooded	3	26	17	4	2	
Breeder gone	1	2	1	1	1	
N total	22	67	40	42	27	198
Failed during incubation						
Unknown (eggs found abandoned)	1	5	2	3	1	
Flooded	2	22	15	3	1	
Predation**	24	56	21	19	18	
N total	27	83	38	25	20	193
Failed after hatching						
Unknown (nestlings found dead)	1	2	2	1	0	
Flooded	2	6	1	2	0	
Breeder gone	2	0	2	0	0	
Parasitised	4	0	0	1	0	
Predation**	24	25	23	15	23	
N total	33	33	28	19	23	136
Success						
Nests found with eggs, ns or fle	96	160	98	68	68	490
Clutches hatched	69	74	60	38	46	287
Clutches fledged	36	43	32	22	25	158

**Direct observations and camera traps identified nest predators as: Gilbert's dragon (n=1, *Amphibolurus gilberti*), Mitchell's water monitor (n=3, *Varanus mitchelli*), Merten's water monitor (n=1, *Varanus mertensi*), yellow-spotted monitor (n = 2, *Varanus panoptes*) and brown-tree snake (n = 1, *Boiga irregularis*). A Brush Cuckoo (*Cacomantis variolosus*) and a Pheasant Coucal (*Centropus phasianinus*) were also seen removing nestlings from a nest.

Table S2. Outputs of all models showing climatic and environmental factors that affect the probability of total nest failure in purple-crowned fairy-wrens. Dataset includes first and re-nesting attempts. Model with lowest AIC included in Table 1 in the main manuscript. Random factor (pair identity) did not contribute to variance of the models. Shown are GLMMs with binomial responses (1/0) using (a) probability of nest not flooding (success=1) (b) probability of nest not succumbing to predation (success=1) and (c) overall probability of nest not completely failing (producing at least one fledgling) (success=1). Shown are coefficients (continuous variables are scaled) and their standard error (s.e.), significant values in bold ($p < 0.05$).

Model	AIC	Intercept	Nest height	Extreme temperature (yes/no)	Average temperature	Extreme rainfall (yes/no)	Average rainfall	Month of the Year	Month quadratic	Habitat quality	Group size
a	132.8	-3.02±0.94	0.90±0.31	0.52±0.98	-0.43±0.19	NA	-0.62±0.11	-0.28±0.22	NA	0.24±0.06	0.10±0.19
	135.8	-3.79±1.02	0.81±0.29	-0.20±0.93	NA	NA	-0.57±0.11	-0.25±0.24	0.15±0.08	0.24±0.06	0.09±0.19
	199.7	-4.43±1.13	0.50±0.24	2.97±0.86	NA	-0.43±0.50	NA	0.35±0.19	0.45±0.09	0.21±0.05	0.17±0.17
	259.5	-0.79±0.59	0.44±0.19	2.83±0.69	-0.42±0.10	-1.39±0.39	NA	-0.03±0.09	NA	0.10±0.04	0.11±0.13
b	484.4	-2.11±0.41	-0.22±0.12	0.94±0.30	-0.18±0.05	-0.82±0.41	NA	0.13±0.04	NA	0.06±0.02	0.13±0.09
	489.6	-2.06±0.41	-0.19±0.12	0.92±0.31	-0.16±0.05	NA	-0.01±0.04	0.13±0.04	NA	0.07±0.02	0.13±0.09
	492.3	-2.27±0.49	-0.21±0.12	0.56±0.27	NA	0.93±0.42	NA	0.09±0.04	0.04±0.02	0.05±0.02	0.11±0.09
	498.4	-2.04±0.49	-0.18±0.12	0.49±0.27	NA	NA	-0.01±0.70	0.08±0.04	0.03±0.02	0.05±0.02	0.11±0.09
c	542.7	-2.52±0.39	-0.08±0.11	0.52±0.35	-0.09±0.04	NA	-0.14±0.03	0.08±0.04	NA	0.09±0.02	0.11±0.09
	546.8	-2.54±0.44	-0.09±0.12	0.24±0.33	NA	NA	-0.15±0.04	0.05±0.04	0.01±0.02	0.08±0.02	0.11±0.08
	573	-2.78±0.44	-0.08±0.11	0.80±0.33	NA	0.05±0.34	NA	0.08±0.04	0.06±0.02	0.08±0.02	0.12±0.08
	574.1	-2.21±0.37	-0.08±0.11	0.95±0.35	-0.15±0.05	-0.15±0.33	NA	0.07±0.04	NA	0.07±0.02	0.13±0.08

* NA= term not included in the model.

Table S3. Climatic and environmental factors that affect the different components of nest success in purple-crowned fairy-wrens. Shown effect of **month as quadratic variable** instead of average temperature. Dataset includes first and re-nesting attempts, excluded unsuccessful nests lost completely to flooding or predation. Random factor (pair identity) did not contribute to variance of the models. (a-c) Results of glmmPQL using a proportion of no. birds hatched/fledged/survived to 6 weeks after fledging from the total no. of eggs, total no. birds hatched, total no. birds fledged respectively. (d) Results of GLMM using number of fledglings as response variable. Shown are model estimates (continuous variables are scaled), their standard error (s.e.), t value and significance (p).

	(a) Hatching success ^a				(b) Fledging success ^a				(c) Post-fledging success ^a				(d) Fledgling recruitment ^b			
No. pairs (nests)	109(208)				97(168)				97(168)				109(188)			
Parameter	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p	Estimate	s.e.	t value	p
Nest height	0.02	0.17	0.14	0.88	0.03	0.15	0.17	0.86	n.a	-	-	-	n.a	-	-	
Extreme temperatures (y/n) ^{c,d}	-0.87	0.4	-2.20	0.03	-0.35	0.44	-0.80	0.43	0.48	0.37	1.28	0.20	0.23	0.18	1.28	0.20
Daily rainfall (mm) ^d	0.16	0.18	0.92	0.36	0.18	0.19	0.96	0.34	-0.42	0.16	-2.71	<0.01	0.07	0.07	1.02	0.30
Month (linear) ^e	-0.19	0.06	-3.38	<0.01	-0.01	0.07	-0.15	0.88	0.17	0.07	2.36	0.02	0.10	0.02	4.29	<0.001
Month (quadratic) ^e	-0.09	0.02	-4.12	<0.001	0.02	0.03	0.47	0.64	-0.03	0.02	-1.26	0.21	0.09	0.09	0.97	0.33
Habitat quality ^f	-0.07	0.05	-1.27	0.21	-0.02	0.03	-0.76	0.45	-0.03	0.03	-0.83	0.40	-0.01	0.01	-1.19	0.23
Group size ^g	-0.09	0.15	-0.63	0.53	0.2	0.11	1.80	0.07	0.12	0.11	1.12	0.27	0.09	0.05	1.84	0.07

^a climate recorded during each stage (e.g. from egg-laying to hatching, from hatching to fledging, from fledging until 6 weeks after), ^b climate recorded since egg-laying until 6 weeks after fledging (total nest cycle), ^c days >42.5°C coded as a factor (yes= experienced at least one day above this temperature, estimate shown relative to zero), ^d values recorded according to the time frame of each stage considered, ^e month (1 = July) at start of nest, ^f habitat quality refers to *Pandanus* cover, ^g group size is number of helpers and adult birds.

Figure S1. Values of daily atmospheric temperatures (°C) from Fitzroy Crossing (weather station = 003093, ~95 Km south West of our study site, data from Bureau of Meteorology- BOM) and daily rainfall data (mm) at our study site Mornington Wildlife Sanctuary (weather station = 002076, data from BOM) showing seasonal variation over the year and days that exceeded upper extreme thresholds (>95th quantile). Each point represents daily values from 1st January 2006 until 31st December 2010 in that period (a) maximum, (b) minimum and (c) average temperature and (d) rainfall. Lines in (a) indicate 42.5°C (95th quantile) and 40°C (90th quantile) and in (d) values above 48.4 mm (95th quantile).

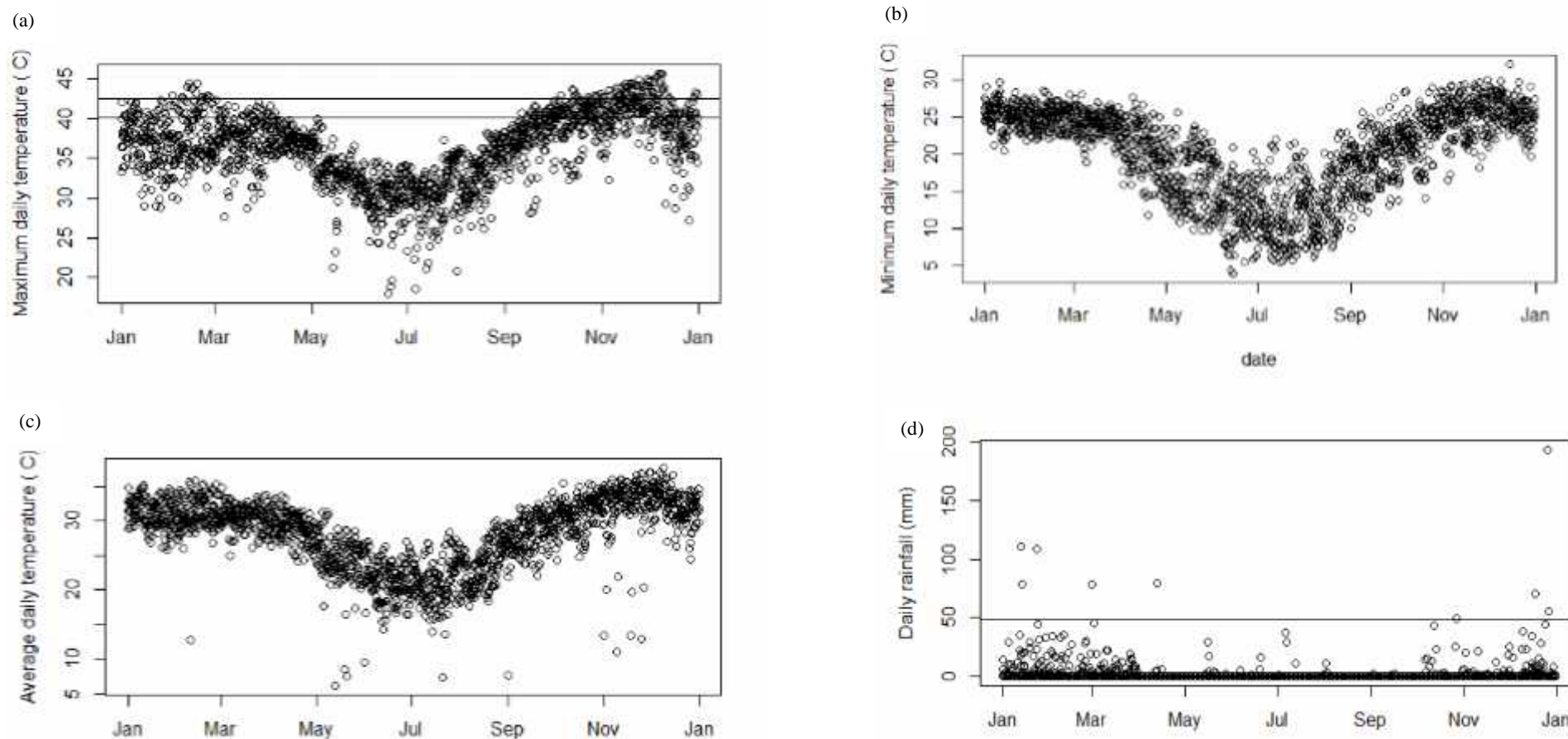


Figure S2. Total number of days per complete decade with river levels exceeding 95th percentile (above 13.36 m) at Dimond Gorge (part of the Fitzroy river, next to our study site) (BOM, Department of Water site number = 802737). Records since 1960 until 2009.

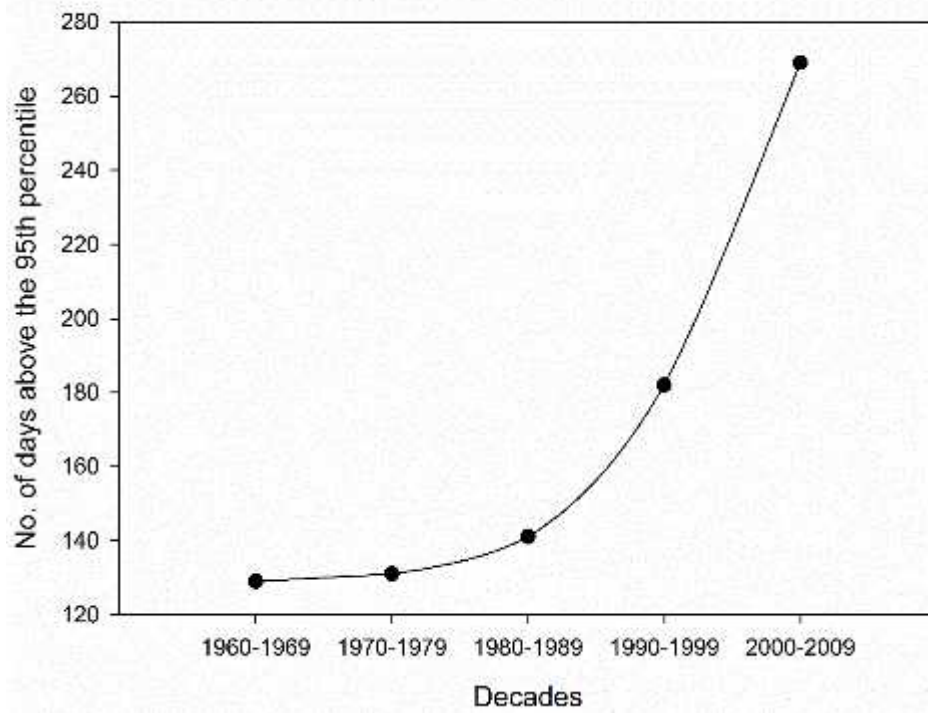


Figure S3. Rainfall records at Fitzroy Crossing (BOM, weather station = 003093, 18.19°S, 125.56 °E, ~ 95 km SW from our study area) since 1910 until 2009. (a) Yearly records of average rainfall (mm). (b) Total number of days per complete decade with daily rainfall exceeding 95th percentile for the area (41.56 mm per day)

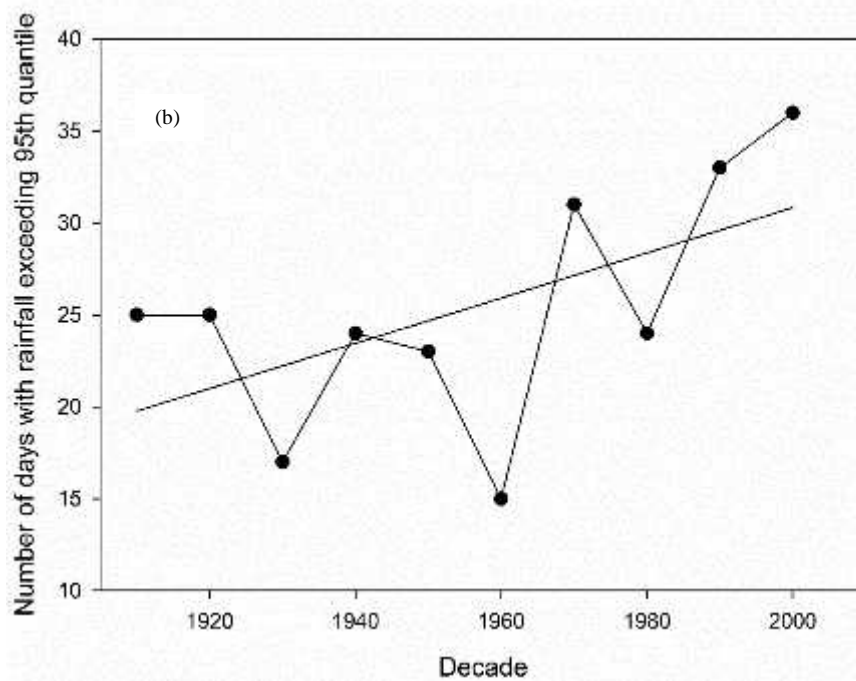
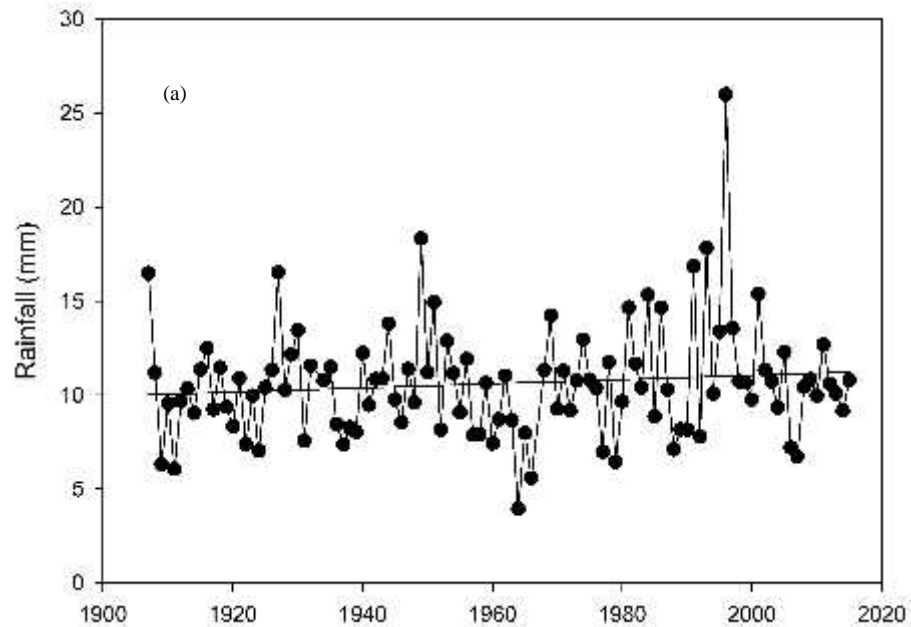
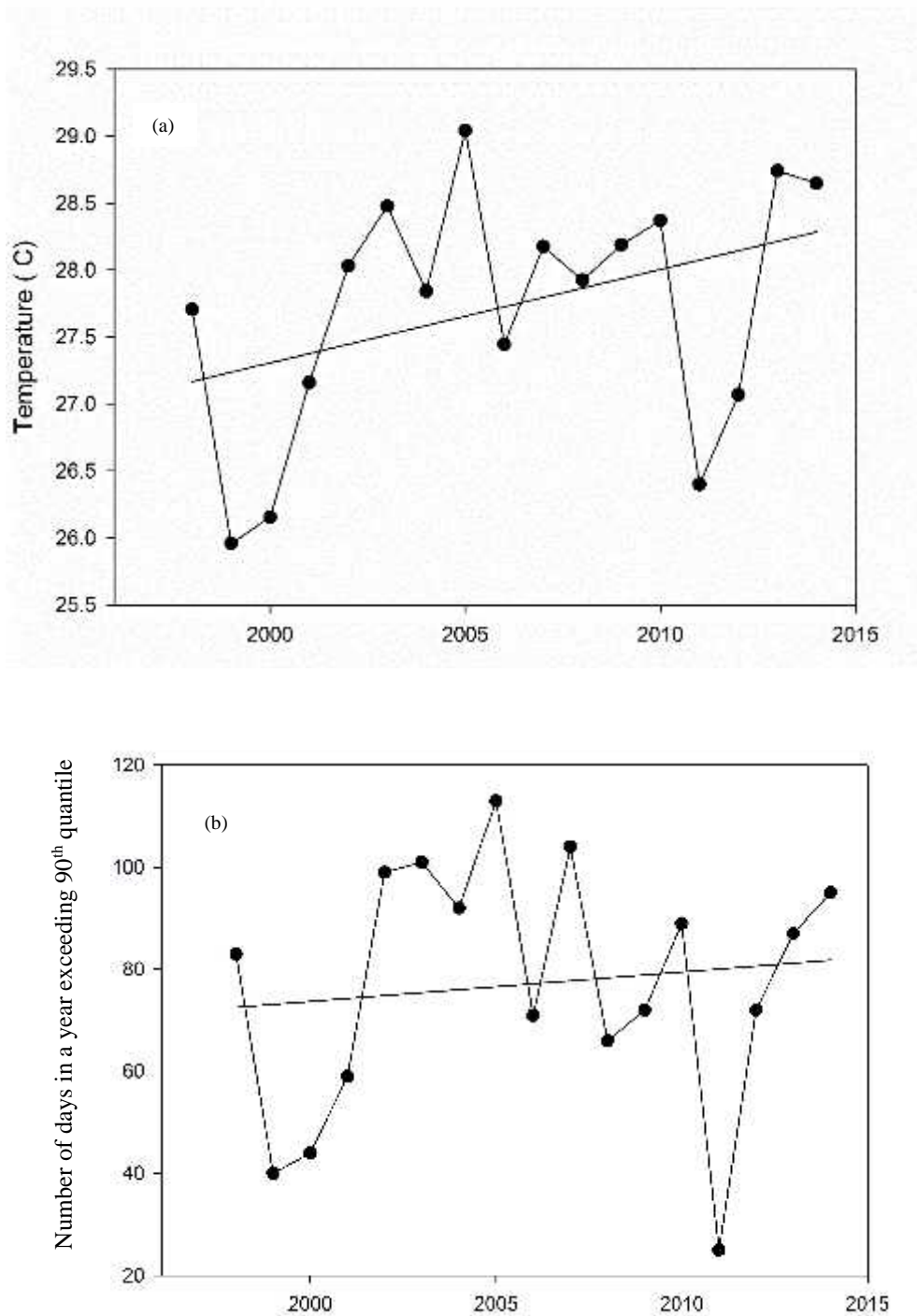


Figure S4. Temperature records at Fitzroy Crossing (BOM, weather station = 003093, 18.19°S, 125.56 °E, ~ 95 km SW from our study area) since 1997 until 2014. (a) Yearly records of average temperature and (b) Total number of days per year exceeding 90th percentile of temperature.



Declaration for Thesis Chapter 3

Declaration by candidate

In the case of Chapter 3, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The key ideas, data collection, data analysis, lab work and writing of the manuscript were my responsibility.	90

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution
Anne Peters	Assistance with writing manuscripts, design of hypotheses, data collection, interpretation of results, feedback on thesis
Michelle L. Hall	Assistance with writing, data collection, interpretation of results.

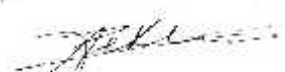
The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work.

Candidate's Signature



Date: 15-10-2016

Main Supervisor's Signature



Date: 15-10-2016

Chapter 3

Limited benefits of mate retention for productivity in a tropical passerine

Abstract

Species that establish permanent pair bonds might be expected to form such relationships because of benefits associated with long pair bonds, such as improvements in breeding performance. Conversely, alternative options might be limited, or have costs, particularly in year-round pair bonded species, in which case no benefits of long pair bonds might be evident. Potential benefits of long pair bonds have been investigated in few tropical species, even though the majority of tropical passerines form stable long-term relationships. Here we investigate potential benefits of long-term pair bonds in a monogamous tropical passerine, *Malurus coronatus*. Our data shows only limited benefits of long pair bonds, in which the likelihood of nest success tended to increase with long relationships. However these effects were relatively weak, and did not translate into higher annual productivity. We also found evidence for between-pairs effects: pairs with longer relationships had higher hatching success, possibly due to death of low quality individuals. Overall, we believe that long-term pair bonds are the by-product of site fidelity and the lack of opportunities for partner change. High quality territories were associated with long pair bonds and the benefits that come from high quality territories are especially important for long-lived species. To detect benefits of long-term pair-bonds, our sample size possibly needs to incorporate more years of data overall, to overcome the effects that climate variation and high predation pressure has on annual reproductive success.

Keywords: monogamy, pair bond investment, breeding experience, survival

Introduction

A monogamous pair bond between a male and a female can be an association to breed only once (i.e. one breeding season) or a bond that continues for several breeding seasons (Cézilly and Nager 1995, Fowler 1995, Black 2001). This latter form of long-term social monogamy is particularly common in birds (Black 1996). The main hypothesis to explain the existence of long-term pair bonds, known as the pair bond investment hypothesis, postulates that breeding success increases over time when remaining with the same partner (Mills 1973, Coulson & Thomas 1983, Bradley et al. 1990, Black 2001, Naves et al. 2007). This effect is a product of improvements in reproduction-related behaviours of a pair, such as sentinel behaviour, foraging efficiency, choice of nest sites and/or defence against predators (Coulson 1966, Black 2001). Mate retention could also be favoured if finding a new partner is costly (Ens et al. 1996, Culina et al. 2014). Although divorce is (often) an adaptive decision (Choudhury 1995, Black 1996, Culina et al. 2014), reproductive success usually decreases after partner change (Culina et al. 2014). Therefore, it is expected that maintaining long-term relationships is an adaptive strategy, particularly if a pair remains together year-round (Fowler 1995).

An alternative explanation for the existence of continuous pair bonds could be that mate retention is a result of permanent territory occupation, in which case no increase in reproductive success might be detected over time (territory fidelity hypothesis) (Freed 1987, Mock and Fujioka 1990). Such a situation might be particularly common in species living in saturated environments, in which availability of vacancies are rare and site fidelity high (Llambias et al. 1998).

The benefits of monogamous long-term pair bonds have been extensively studied in long-lived species living in temperate regions (Black 1996). However, to date, there is limited research on potential benefits of long-term monogamy in tropical birds. This is despite the

fact that year-round territoriality and long pair bonds are common in tropical species (Fowler, 1995, Stutchbury and Morton 2001, Tobias et al. 2011). Moreover, due to their slow life-histories and relatively long lifespan, effects of long relationships on productivity might be common for tropical passerines (Hammers et al. 2012).

Individual breeding experience can be an important determinant of productivity of a pair if individual reproductive performance increases with breeding experience (Forslund and Part 1995, van de Pol et al. 2006, Sanchez-Macouzet et al. 2014). Thus, disentangling effects of pair duration and breeding experience is the first step to understand if any improvement in reproduction is related to long relationships (Fowler 1995, Naves et al. 2007). While some studies have shown that individual breeding experience can matter, it appears that pair bond duration is more relevant for some species (e.g. Black et al. 2001, van de Pol et al. 2006).

Here we analysed 10 years of data in a tropical cooperatively breeding bird that establishes long-term pair bonds, the purple-crowned fairy-wren *Malurus coronatus*. Purple-crowned fairy-wrens defend their territories year-round and are socially and nearly genetically monogamous (Kingma, et al. 2009, 2013). Furthermore, partner change is rare, since survival is high and divorce rates are low (8% annual divorce rate on average, Hidalgo Aranzamendi et al. 2016). We tested if there is an effect of pair bond duration on reproductive performance or survival of breeders while taking into account individual breeding experience.

Methods

Study species

Purple-crowned fairy-wrens are cooperative breeders that nest year-round, although there are two identifiable breeding peaks in the population: one during the wet season (Dec-Mar) and occasionally one peak at the dry season (Jun-Aug) (Peters et al. 2013). All birds in the study population were colour-banded for individual identification. Males are more philopatric than

females but many breeding females (59% of breeders) recruit from local nests (Hidalgo Aranzamendi et al. 2016). Only the dominant male and dominant female reproduce. Both dominants and a variable number of subordinates (0-10) occupy year-round territories that occur exclusively in riparian vegetation of the palm-like *Pandanus aquaticus*. Breeders remain in close proximity to each other most of the time and they use duets for territorial defence (Hall and Peters 2008, 2009). Divorce rate is low at the population level (8% on average), in which a third of divorces occur to end incestuous relationships (i.e. between first-degree relatives, 64% of relationships end in divorce (18 pairs); Hidalgo Aranzamendi et al. 2016). Extra-pair paternity is low among non-incestuous pairs (3.3% population average) (Kingma et al. 2009, 2013). Age at first reproduction is highly variable: males started reproducing between 6 months up to 4.2 years ($n = 85$, mean = 18 months) and females between 4 months up to 4.5 years ($n = 74$, mean = 26 months, unpubl. data). Pairs can remain together up to 8 consecutive years, on average pair bonds last 2.3 years (median = 1.8 years) and annual survival for breeders in this population is 82 ± 4.6 SD % for males and 78 ± 5.3 SD % for females (Kingma et al. 2009, unpubl.data 2005-2015).

Data collection

Since 2005 until 2010, all reproductive events were followed closely (all nesting attempts recorded until failure or when fledglings survived to 12 weeks old) starting with 38 territories that eventually increased to 69 by the end of 2015, as a result of increase in territory density. From 2010 onwards, two yearly censuses were conducted after the wet season and at the end of the dry season following the reproductive peaks of the population. During these, all birds were resighted, and the number and approximate age of fledglings, if present, was recorded. All fledglings were banded, genotyped and had paternity assigned (details found in Hidalgo

Aranzamendi et al. 2016). Birds were called dead if not resighted in two consecutive censuses. Estimates of pair bond duration using the biannual census method used in 2011-2015 closely resemble estimates from the weekly census method used between 2005 and 2010 ($r = 0.98$) (see Hidalgo Aranzamendi et al. 2016 for details).

Reproductive performance was measured for each pair as likelihood of nest success (at least one chick fledging = yes), clutch size (range 2-4, mean = 2.93 ± 0.05 SD eggs), hatching success (proportion of eggs that hatched, range = 0.66 to 1, mean = 0.89 ± 0.24 SD of eggs hatched, excluding total nest failure) and fledging success (proportion of chicks that fledged, range = 0.25 to 1, mean = 0.83 ± 0.26 SD of hatched eggs fledged, excluding total nest failure) for each year between 2005-2010. Fledging success could be only determined for nests in which at least one egg hatched. Annual fledgling production (the number of fledglings surviving to independence ~9 weeks old, range = 0-6, mean = 1.97 ± 1.21 SD) was measured for each year from 2005-2015. We also tested annual fledgling production with a subset of pairs from 2005-2010 to test more accurate estimates of pair bond duration.

Although results were similar, statistical power decreased with this reduced sample and we show estimates from 10 years of data for annual fledgling production.

Pair bond duration was quantified as the number of consecutive months a male and a female were together. We retrieved the breeding history of 96 males and 84 females with known pair bond duration from 2005-2015 ($n = 194$ pairs; some individuals occurred with multiple partners) and quantified reproductive performance per year (starting from July 1st). We assumed that females entering the breeding population (immigrants) had no previous breeding experience ($n = 32$). From the total sample, 85 males and 74 females had known hatch date (excluding immigrant females), the rest of birds were part of the original study population and were already breeders or subordinates in their initial capture year. For males and females with known hatch date, we calculated breeding experience as the number of

months elapsed since the first reproductive attempt. In this subset of birds, age and breeding experience (time as a breeder) were highly correlated ($r = 0.90$), precluding independent assessment of their effects, we assume that this situation is most likely true for all birds in the population. We first tried all statistical models using age (in months, as continuous) instead of breeding experience (in months) and commensurate with the high correlation between age and breeding experience, results were nearly identical (Table S1 show results with breeding experience). Because the analysis using breeding experience as a continuous variable suggested that the effect of breeding experience was evident only in the first year as a breeder, we coded breeding experience as a factor, i.e. whether or not individuals had successfully fledged offspring previously. This allowed us to include birds with known previous reproductive success, but with unknown exact duration of breeding experience and to extend our sample size. The association between female and male breeding experience coded in this way was not significant ($r < 0.40$, $\chi^2 = 1.05$, $p = 0.31$). Incestuous pairs were excluded from all analyses, since they are more likely to divorce and no incestuous relationships lasted longer than a year ($n = 29$ pairs, Hidalgo Aranzamendi et al. 2016), plus incestuous pairs have high rates of hatching failure (Kingma et al. 2013).

Statistical procedure

We tested if there is an effect of pair bond duration on indicators of reproductive performance using generalized linear mixed models (GLMM), namely (A) probability of nest success (failure = predation, predation is the major source of failure (57%), other sources of failure are due to stochasticity of climate variables, Fig. 1, Chapter 2), (B) clutch size, (C) hatching success, (D) fledging success and (E) annual production of recruits. A relationship between clutch size and breeding experience has been recorded for other species (Fowler 1995). A

correlation between pair bond duration and likelihood of nest success, hatching or fledging success or annual fledgling production would indicate an improvement in coordination skills of the pair members in nest defence or improvement in foraging efficiency as a benefit of mate retention (van de Pol 2006, Lv et al. 2016). Likelihood of nest predation was fitted with a binomial distribution, in here a successful nest ($n = 287$) produced at least one fledgling (success = 1), failed nests ($n = 196$) were predated (failure = 0). Clutch size (1-4) and annual fledgling production (0-6, calculated from total nest attempts of the pair in a year) were fitted with Poisson distributions and hatching success and fledging success (proportion hatched/fledged, non-hatched/non-fledged) were fitted with binomial distributions using the command *cbind* and *lme4* (Bates 2014).

Pair bond duration (months) was entered as a linear and quadratic factor to test for non-linear effects of pair bond duration on performance (i.e. a quadratic effect could show a decline at old ages). To disentangle within-pair and between-pair effects of pair bond duration, we added maximum pair bond duration as a covariate in a separate model; this allows to distinguish if effects of pair bond duration are due to selective disappearance of particular pairs, e.g. with low productivity, from the population or due to changes in pair productivity with changing pair bond duration (van de Pol et al. 2006, van de Pol 2006). Models were first tested with GLMs with quasi-binomial distributions to account for overdispersion. If models were not overdispersed we proceeded with GLMMs including the random terms. Other curvilinear function (logarithmic) of pair bond duration were tried instead of both linear and quadratic factors (van de Pol 2006), to test if reproductive performance reflects a non-linear response (e.g. increase in reproductive performance reaches a plateau after some years together). This function was not significant in any model (results not shown). Since repeated measurements of the same pair were taken and individuals were also found in different pair combinations, we included male and female identity and year as cross-classified random

effects with individual measurements nested within these random effects (for details van de Pol and Verhulst 2006, van de Pol et al. 2006).

Because territories with more vegetation cover and larger groups have higher productivity (Kingma et al. 2011a, Chapter 2), both variables were included in all models and models were also tested using only these two variables as a baseline model (i.e. excluding effects of pair bond duration or breeding experience) and then outputs of alternative models were compared to baseline model. We also included breeding experience of the breeders (as factor 1/0, in which 1 = fledged chicks in a prior year). Correlations between co-variables were all low ($|r| < 0.54$). We present models based on AIC coefficients (top models are those < 2 units of difference from the null model).

We also tested whether long term pair bonds were associated with territory quality (an index of *Pandanus* vegetation cover 1-20, Chapter 2), using a GLMM, we entered one value for territory quality for each pair, and their maximum pair bond duration was included as a linear and quadratic factor; also initial group size as a covariate. Since males and females were found in different pair combinations, they were included as random terms. Finally, we tested the effect of pair bond duration (months) on annual probability of survival of breeders. For this, we included the last year for each pair with known pair bond duration (pair bonds could end due to divorce, death of focal bird, death of mate, or be ongoing) and quantified individual survival probability over the following year. Survival to 30th June of the next year (x = initial year starting 1st July, $x+1$ = year finishing at 30th June) was included as a dependent variable in a GLM with binomial distribution. We included pair bond duration (months) on 1st July of year x as a linear and quadratic term, fledgling production in last year $x-(x+1)$, group size and territory quality (at initial year starting on 1st July = year x) as fixed factors. We did not include maximum pair bond duration due to collinearity with age and breeding experience. Males and females were analysed separately, and since survival can

depend on age, we included age as a covariate and analysed birds of known age only (see Table S2). We repeated these models using breeding experience as a factor and with the extended sample size to include birds with unknown hatch date, obtaining similar results. Continuous variables from all models were scaled. All analyses were done in R 3.1.2 (R Development Team 2016).

Results

Models without pair bond duration and breeding experience showed the lowest AIC coefficients in most cases (Tables 1 and 2), suggesting that pair bond duration and breeding experience or age of breeders do not increase reproductive output over time. We detail here outputs of models that included both terms and specific cases in which some level of significance was found. The majority of nest attempts failed mostly due to predation (57% of nests, see also Chapter 2). The likelihood of nest predation tended to decrease with increasing pair bond duration (positive linear effect, $p = 0.09$), however it increased again for very long pair bonds (i.e. negative quadratic effect, $p = 0.05$, Fig. 1). Breeding experience of the pair did not affect likelihood of nest predation (Table 1) but larger groups had higher probability of nest success (Table 1). We identified no between-pairs effect on likelihood of nest predation (no effect of maximum pair bond duration), meaning that pairs with longer pair bonds did not systematically differ in nest predation rates.

Pair bond duration did not affect clutch size, hatching success or fledging success (Table 1). Although hatching success did not change as pairs stayed together longer (Table 1), we did find a positive between-pairs effect on hatching success (i.e. positive effect of maximum pair bond duration, $p = 0.04$) indicating that pairs with higher hatching success stayed together for longer (Table 1). Annual fledgling production did not vary with pair bond duration (no linear or quadratic effect, Table 2), or with breeding experience (Table 2). However, territories of

higher quality tended to recruit more fledglings (Table 2, $p = 0.08$). The best supported models did not include breeding experience, for most reproductive indicators (Tables 1 and 2).

We found a trend for territories of higher quality being held by pairs with longer relationships (positive linear effect, $p = 0.07$, Table 3) but this decreased for pairs that stayed together for very long (i.e. negative quadratic effect, $p = 0.03$, Table 3, Fig. 2). Similarly, territories of higher quality had larger groups (Table 3, $p = 0.02$).

Longer pair bonds were not associated with higher likelihood of surviving the following year (Table 4), although there was a trend for a negative linear ($p = 0.07$) and positive quadratic ($p = 0.08$) effect of pair bond duration on male survival (Table 4). Also, we found a trend for lower survival for experienced females ($p = 0.06$, Table 4).

Discussion

We found limited evidence for positive effects of long pair bonds on productivity in purple-crowned fairy-wrens. These benefits occurred only at early stages of reproduction, in which the likelihood of nest success tended to increase over the first years of relationship and then decrease with longer pair bonds. Increased likelihood of nest success with longer pair bonds could be related to improvements in nest placement by females. However, this does not seem particularly likely, because (1) no effect of individual breeding experience was found and (2) although nest predation risk might be slightly reduced by nest placement at lower heights, this effect is small and counterbalanced by increased risk of nest flooding (Chapter 2).

Alternatively, pairs breeding together for several years could improve pair compatibility in defending nests against predators, something that has been demonstrated for other species (Black 2001, Griggio and Hoi 2011, Weiß et al. 2010, Leu et al. 2015). Nest predation is

responsible for the majority of nests losses in purple-crowned fairy-wrens and successful nest defence would be a key benefit for pairs that stay together for a long time. However, this increase in nest survival was moderate and detectable over the first years of relationship only (Fig. 1). Nest survival declined again for longer pair bonds, which might be related to age, and an indication of senescence (Fig. 1, Table 1). However, sample sizes for very long pair bonds are reduced and this decline might be driven by relatively few pairs (Fig. 1).

Pairs that remained together longer had higher hatching success (Table 1), as is demonstrated by the positive between-pair effect of pair bond duration (maximum pair bond duration) on hatching success. This relationship suggests selective disappearance of low quality pairs (pairs with at least one low-quality member), since pairs with short pair bond duration are disproportionally the result of partner's death (Chapter 4). Although, we found no strong effects of pair bond duration on adult survival (Table 4), males tended to survive less well in short to mid-range pair bonds, with a trend for improved survival at long pair bonds (quadratic effect). Although there is evidence that long-term pair bonds could involve survival benefits in other species (Stutchbury and Morton 2001), annual survival in purple-crowned fairy-wrens is high (up to 81% on average for both sexes, Kingma et al. 2009), which might hinder detection of survival benefits of long pair bonds.

Alternative benefits, rather than increased productivity or survival, explain the existence of long-pair bonds, and our results are in agreement with the territory fidelity hypothesis, Freed 1987, Mock and Fujioka 1990, Tobias et al. 2016). This hypothesis suggests that long-term pair bonds effectively are a by-product of maintaining or permanently using the same site or territory (Ens et al. 1995, Morton 1996, Black 2001, Gill et al. 2007, Tobias et al. 2016). This could well apply to purple-crowned fairy-wrens, since pairs that stayed together longer tended to occupy territories of higher quality (Table 3). In this species, breeding pairs occupy the same territory for the duration of their pair bond and pairs switching territories together

has never been recorded. As is common in cooperative breeders (Komdeur 1996), purple-crowned fairy-wrens also experience strong constraints on available territories (breeding vacancies) which is evidenced by delayed breeding and the formation of long-term, up to one year, incestuous pair bonds, despite significant costs of inbreeding (Kingma et al. 2009, 2013, Hidalgo Aranzamendi et al. 2016). Also close pair coordination is important in territorial defence (Hall and Peters 2009). Moreover, in purple-crowned fairy-wrens, high quality territories are associated with many long-term benefits: high quality territories decrease the likelihood of nest predation (Chapter 2), drive breeder dispersal in divorcing females (Chapter 4), tend to recruit more fledglings and hold larger groups (Kingma et al. 2010, 2011b, Table 2) indicating that these could be attractive for subordinates to delay dispersal or disperse to. All this could explain why pairs that held higher quality territories stayed together for longer. However, we found that pairs with very long pair bonds hold lower quality territories, as evidenced by the negative quadratic relationship between pair bond duration and territory quality (i.e. quadratic effect, Table 3, Fig. 2). This quadratic relationship could be a reflection that pairs with very long relationships stayed together due to constraints on availability of any alternative territories, showing that owning a territory is constrained by opposite forces. Although most of our results offer support for the territory fidelity hypothesis among all the other hypotheses tested, this option also has less clear predictions since individual quality or survival (and thereby pair bond duration) could be interlaced with territory quality. Furthermore, territory quality and productivity of the territory, as there is a positive relationship between productivity and group size (Kingma et al. 2010) and between territory quality and productivity (Table 2) are inherently linked and thus assumptions on which is the reason for long term pair bonds based on those two indicators might be circular.

Although it is assumed that inexperienced breeders are less effective defending territories or achieving successful reproduction (Grigio and Hoi 2011, Ihle et al. 2015, Lv et al. 2016), we did not find an effect of breeding experience on any aspect of reproductive success and in fact, models were better supported when these parameters were not included (Table 1). This could be because in species living in cooperative societies, individual effects of breeding experience might be less important or harder to detect (DuVal 2011). In such species, breeding experience can be indirectly gained by helping, in this situation, many of the skills required to improve reproductive success, such as sentinel behaviour and better defence against predators might be gained before acquiring their own offspring while helping raising younger group members (DuVal 2013).

In summary, we found that mate retention in purple-crowned fairy-wrens conferred limited reproductive benefits over time. We found limited evidence to support the hypothesis that long-term pair bonds are maintained to increase productivity. Two other studies of tropical birds similarly reported no apparent benefits of mate retention for reproduction (House wren Freed 1987, Pinyon jays Marzluff and Balda 1988), suggesting a lack of benefits of mate retention on productivity for tropical species more generally. Instead, it seems that the need for dual defence of high quality territories could be a priority over reproductive benefits.

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Table 1. Effect of pair bond duration (PBD), in months and individual breeding experience (BE, as factor⁺) on productivity. (A) Probability of nest success (predation = 0, success = 1). (B) Clutch size, (C) hatching success (proportion eggs hatching) and (D) fledging success (proportion chicks fledging). Reproductive estimates from 2005-2010. n = # nests, F = # females, M = #males, Y = # years. Random factors (female and male identity and year) did not contribute to variation in any model. Models arranged by AIC values; null models (without pair bond duration and breeding experience) had higher support, top models (< 2 ΔAIC) are those compared in relation to null model, p < 0.05 in bold.

(A) Nest success	n135, 50 F, 50 M, 6Y																	
AIC	192.3			192.10			193.70			195.40			196.90			198.20		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	0.12	0.17	0.46	0.01	0.19	0.94	0.01	0.19	0.94	0.47	0.57	0.41	0.48	0.58	0.41	0.13	0.49	0.78
Territory quality	0.01	0.18	0.97	0.12	0.20	0.55	0.08	0.21	0.70	0.12	0.21	0.55	0.08	0.22	0.71	0.08	0.19	0.69
Group size	0.35	0.18	0.05	0.57	0.24	0.02	0.58	0.24	0.02	0.60	0.25	0.01	0.61	0.25	0.01	0.52	0.22	0.02
PBD				1.06	0.63	0.09	1.15	0.65	0.08	1.52	0.85	0.07	1.61	0.87	0.06	-0.17	0.25	0.48
PBD ^2				-1.22	0.62	0.05	-1.22	0.62	0.05	-1.54	0.74	0.04	-1.55	0.75	0.04			
PBD (max)							0.16	0.24	0.50				0.17	0.24	0.49			
BE F (y/n)										0.27	0.51	0.59	0.29	0.51	0.57	0.05	0.48	0.91
BE M (y/n)										0.38	0.56	0.50	0.37	0.56	0.51	0.15	0.48	0.75
(B) Clutch size	n187, 55F, 53M, 6Y																	
AIC	681.1			685.00			685.40			685.60			687.60			687.80		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	1.27	0.04	<0.001	1.27	0.04	<0.001	1.26	0.04	<0.001	1.35	0.11	<0.001	1.36	0.12	<0.001	1.36	0.12	<0.001
Territory quality	0.03	0.04	0.52	0.03	0.04	0.52	0.01	0.04	0.80	0.02	0.04	0.58	0.02	0.04	0.60	0.01	0.04	0.90
Group size	0.03	0.04	0.41	0.03	0.04	0.46	0.03	0.04	0.46	0.04	0.04	0.38	0.04	0.04	0.37	0.04	0.04	0.37
PBD				-0.02	0.13	0.86	-0.06	0.13	0.63	0.02	0.05	0.66	0.05	0.16	0.75	0.01	0.17	0.95
PBD ^2				0.02	0.12	0.85	0.03	0.12	0.80				-0.03	0.14	0.84	-0.02	0.14	0.88
PBD (max)							0.06	0.05	0.20							0.07	0.05	0.18
BE F (y/n)										0.02	0.10	0.87	0.01	0.11	0.93	0.02	0.11	0.89
BE M (y/n)										-0.12	0.10	0.23	-0.13	0.11	0.23	-0.15	0.11	0.21

(C) Hatching success n98, 40F, 44M, 6Y																		
AIC	143			143.40			145.90			146.20			147.00			149.00		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	2.51	0.42	<0.001	2.60	0.42	<0.001	1.94	0.72	<0.001	2.54	0.43	<0.001	1.93	0.69	0.01	1.89	0.78	0.02
Territory quality	-0.06	0.25	0.79	-0.05	0.23	0.83	-0.08	0.24	0.75	0.07	0.25	0.80	0.04	0.26	0.88	0.04	0.26	0.89
Group size	0.14	0.26	0.59	0.08	0.26	0.76	0.05	0.27	0.87	0.04	0.29	0.90	0.01	0.29	0.98	0.01	0.29	0.99
PBD				0.19	0.71	0.78	-0.40	0.89	0.65	0.50	0.71	0.48	-0.03	0.34	0.92	-0.12	0.96	0.90
PBD ^2				-0.46	0.67	0.49	-0.09	0.77	0.91	-0.31	0.66	0.64				0.08	0.78	0.92
PBD (max)				0.81	0.39	0.04	0.84	0.40	0.03									
BE F (y/n)							0.79	0.65	0.23				0.75	0.64	0.24	0.78	0.72	0.28
BE M (y/n)							0.21	0.59	0.72				0.19	0.61	0.75	0.22	0.65	0.74
(D) Fledging success n97, 48F, 47M, 6Y																		
AIC	204.60			205.3			205.10			206.60			207.10			209.10		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	1.20	0.30	<0.001	1.17	0.32	<0.001	0.93	0.51	0.07	1.19	0.30	<0.001	0.92	0.54	0.09	0.91	0.55	0.09
Territory quality	-0.04	0.15	0.82	-0.02	0.14	0.88	-0.02	0.15	0.92	-0.03	0.15	0.82	-0.02	0.15	0.92	-0.01	0.15	0.94
Group size	0.01	0.17	0.96	0.12	0.17	0.50	0.03	0.18	0.88	0.01	0.17	0.96	-0.03	0.18	0.88	-0.03	0.18	0.87
PBD	0.56	0.52	0.28				0.30	0.25	0.22	0.56	0.53	0.29	0.28	0.66	0.68	0.28	0.66	0.68
PBD ^2	-0.17	0.57	0.76							-0.17	0.57	0.76	0.02	0.64	0.97	0.03	0.64	0.96
PBD (max)										-0.01	0.18	0.99				-0.02	0.18	0.93
BE F (y/n)							-0.13	0.40	0.75				-0.13	0.41	0.76	-0.12	0.42	0.77
BE M (y/n)							0.50	0.41	0.22				0.51	0.43	0.24	0.51	0.44	0.24

* Estimates are relative to 1.

*Experienced breeders are those that fledged at least one offspring before (1 = experienced breeder, 0 = first-time breeder).

Table 2. Effect of pair bond duration (PBD, in months) and individual breeding experience (BE, as factor⁺) on annual fledgling production (# fledglings / year). Reproductive estimates from 2005-2015. B = # breeding pair-years, F = # females, M = #males, Y = # years. Random factors (female and male identity and year) did not contribute to variation in any model. The top models (< 2 Δ AIC) are shown, $p < 0.05$ in bold

(A) Annual fledgling production																			
B201, 84F, 95M, 10Y																			
AIC	635.2			638.10			639.80			639.90			641.50			643.20			
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	
Intercept	0.63	0.09	<0.001	0.63	0.09	<0.001	0.63	0.09	<0.001	0.69	0.13	<0.001	0.70	0.13	<0.001	0.70	0.13	<0.001	
Territory quality	0.1	0.05	0.05	0.09	0.05	0.07	0.09	0.05	0.09	0.09	0.05	0.08	0.09	0.05	0.08	0.09	0.05	0.09	
Group size	0.08	0.05	0.12	0.06	0.06	0.26	0.06	0.06	0.25	0.06	0.06	0.26	0.07	0.06	0.22	0.07	0.06	0.22	
PBD				0.10	0.14	0.47	0.06	0.16	0.73	0.07	0.06	0.25	0.16	0.16	0.33	0.11	0.18	0.54	
PBD ^2				-0.05	0.14	0.70	-0.04	0.14	0.77				-0.09	0.15	0.55	-0.08	0.15	0.62	
PBD (max)							0.05	0.08	0.56							0.04	0.08	0.61	
BE F (y/n)										-0.07	0.13	0.61	-0.08	0.14	0.54	-0.09	0.14	0.55	
BE M (y/n)										-0.02	0.14	0.86	-0.04	0.14	0.80	-0.03	0.14	0.84	

* Estimates are relative to 1.

⁺Experienced breeders are those that fledged at least one offspring before (1 = experienced breeder, 0= first-time breeder).

Table 3. Longer pair bonds (PBD max, in months) tended to be associated with territories of higher quality, although very long pair bonds had territories of lower quality (i.e. quadratic effect). Each pair is included once, since pairs hold the same territory for several years. Males and females were found in different pair combinations and included as random terms; these did not contribute to variance of model. $P < 0.05$ in bold

Territory quality	n = 89		
Fixed effects	Estimate	SE	p
Intercept	9.66	0.5	<0.001
Group size	1.19	0.50	0.02
PBD (max)	2.90	1.61	0.07
PBD (max) ^2	-3.48	1.61	0.03

Table 4. Longer previous pair bond duration (PBD, in months, census 1 July year x) was not associated with greater likelihood (1/0) of surviving the following 12 months (to 1 July year x + 1) for males (M) or females (F). Individual breeding experience (BE, as factor⁺) in females tended to be associated with a lesser likelihood of surviving the following 12 months, possibly an effect of age. Results from a GLM with binomial distribution. Estimates are relative to 1, n = # individuals. p < 0.05 in bold

Models	Females n = 67			Males n = 77		
	Estimate	SE	p	Estimate	SE	p
Intercept	2.28	0.58	<0.001	2.18	0.57	<0.001
Fledgling production	0.07	0.25	0.77	0.52	0.32	0.10
Territory quality	-0.04	0.25	0.88	0.27	0.30	0.38
Group size	0.46	0.32	0.15	-0.49	0.32	0.13
PBD	0.52	0.81	0.52	-2.02	1.10	0.07
PBD ^2	-1.02	0.78	0.19	1.95	1.11	0.08
BE F (y/n) ^{*+}	-1.31	0.70	0.06			
BE M (y/n) ^{*+}				-0.03	0.75	0.97

* Estimates are relative to 1.

⁺Experienced breeders are those that fledged at least one offspring before (1 = experienced breeder, 0 = first-time breeder).

Figure 1. The likelihood of nest success (success = yes, predation = no) increases with longer pair bonds, however this effect decreases with pair bonds that last very long. This effect is independent of individual breeding experience. Shown are predicted values of a generalized linear mixed model. Other fixed terms were territory quality and group size. Model shown includes pair bond duration as a quadratic term, there were no effects of maximum pair bond duration as a covariate (to control for selective disappearance).

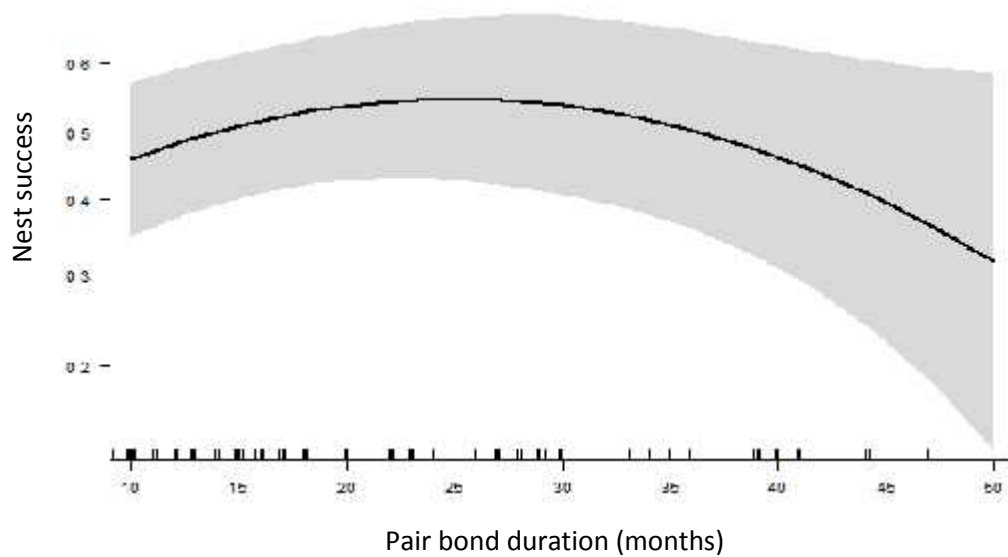
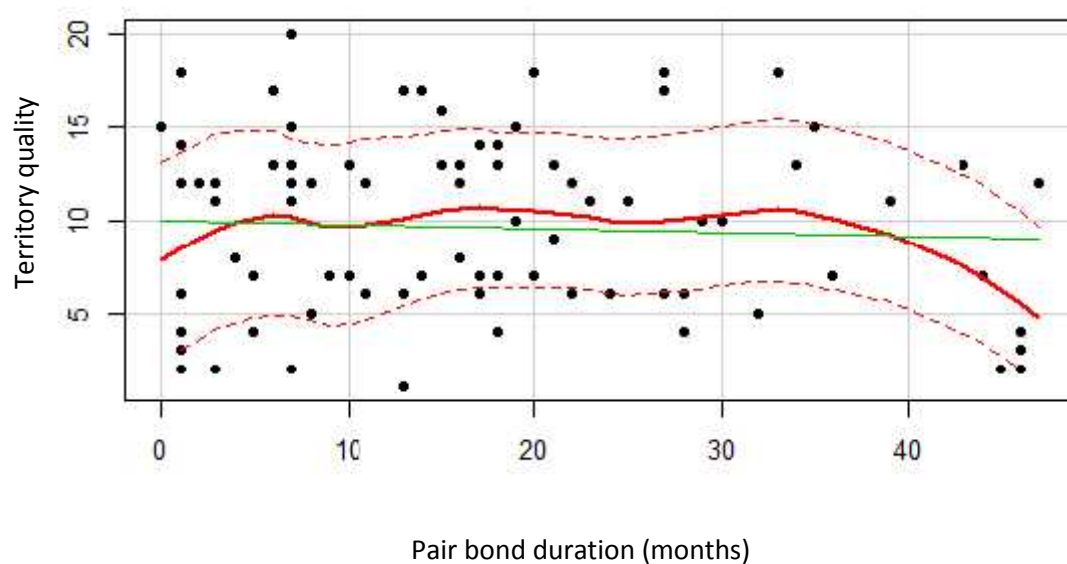


Figure 2. Territories of higher quality are held by pairs that stay together longer (positive linear effect $p = 0.07$) however this effect decreases with pair bonds that last very long (negative quadratic effect, $p = 0.03$). Territory quality is an index of *Pandanus* vegetation cover ranging from 1-20. Shown are raw values, other covariate in generalized linear mixed model was group size. Red line shows best fit to raw data and dotted lines show intervals of confidence, green line shows the best linear fit. Males and females were found in different combinations and included as random terms that did not contribute to the variance of the model.



Supplementary material

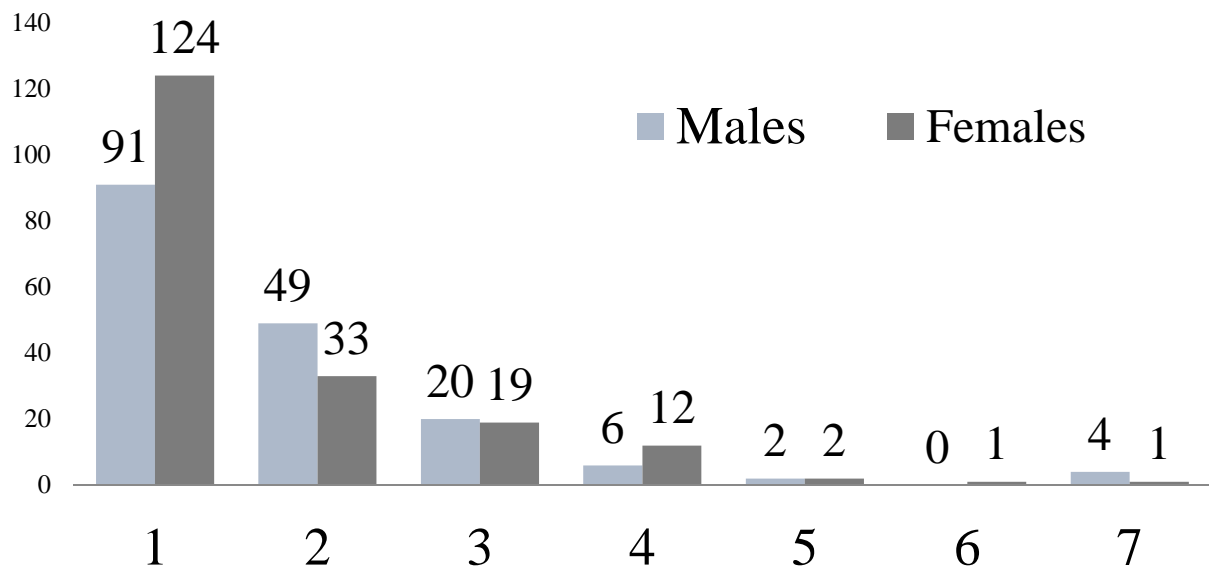
Table S1. Effect of pair bond duration (PBD) and individual breeding experience (BE as continuous variable) on productivity. (A) Probability of nest success (predation = 0, success = 1). (B) Clutch size, (C) hatching success (proportion eggs hatching) and (D) fledging success (proportion chicks fledging) (E) annual fledgling production. Reproductive estimates from 2005-2010 for A-D, until 2015 for E. n = # nests, F = # females, M = #males, Y = # years, B = # breeding pair-years. Random factors (female and male identity and year) did not contribute to variation in any model. Models arranged by AIC values; all models shown.

(A) Nest success															
n78, 31F, 37M, 6Y															
AIC	119.4			121.4			122.6			123.6			124.5		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	0.08	0.24	0.72	0.09	0.24	0.72	0.08	0.23	0.73	0.09	0.24	0.72	0.08	0.23	0.73
Territory quality	0.02	0.24	0.91	0.03	0.25	0.90	0.06	0.27	0.84	0.03	0.25	0.90	0.06	0.28	0.84
Group size	0.43	0.32	0.19	0.43	0.33	0.19	0.37	0.31	0.23	0.43	0.33	0.19	0.38	0.31	0.23
PBD	1.21	0.78	0.12	1.20	0.80	0.13	0.48	0.58	0.41	1.21	0.79	0.13	-0.48	0.58	0.41
PBD ^2	-1.34	0.78	0.08	-1.35	0.78	0.08				-1.35	0.78	0.08			
PBD (max)				0.02	0.32	0.93				0.03	0.32	0.93			
Breeding experience F							-0.03	0.38	0.95				-0.03	0.38	0.95
Breeding experience M							0.44	0.46	0.34				0.44	0.47	0.34
(B) Clutch size															
n112, 36F, 39M, 6Y															
AIC	415.7			417			417.7			419.6			421.1		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	1.25	0.05	<0.001	1.25	0.05	<0.001	1.25	0.05	<0.001	1.25	0.05	<0.001	1.30	0.05	<0.001
Territory quality	0.02	0.05	0.66	0.01	0.05	0.78	0.01	0.06	0.81	0.02	0.06	0.79	0.01	0.06	0.86
Group size	0.09	0.06	0.16	0.09	0.06	0.15	0.08	0.06	0.17	0.08	0.06	0.20	0.08	0.06	0.19
PBD	-0.07	0.15	0.64	-0.10	0.15	0.52	-0.03	0.11	0.75	-0.07	0.17	0.67	-0.11	0.18	0.55
PBD ^2	0.04	0.14	0.78	0.04	0.14	0.78				0.04	0.14	0.77	0.04	0.14	0.78
PBD (max)				0.05	0.07	0.44							0.05	0.07	0.46
Breeding experience F							0.02	0.08	0.82	0.02	0.08	0.82	0.01	0.08	0.88
Breeding experience M							-0.01	0.09	0.90	-0.02	0.08	0.82	-0.01	0.09	0.89
(C) Hatching success															
n59, 26F, 31M, 6Y															
AIC	93.30			93.90			94.80			95.0			95.30		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	2.72	0.56	<0.001	2.83	0.59	<0.001	2.73	0.57	<0.001	2.85	0.59	<0.001	2.70	0.55	<0.001
Territory quality	-0.20	0.39	0.75	-0.13	0.39	0.74	0.11	0.37	0.76	-0.14	0.37	0.7	0.06	0.33	0.85
Group size	0.14	0.40	0.73	0.25	0.44	0.57	0.40	0.45	0.38	0.27	0.45	0.54	0.40	0.44	0.38
PBD	-0.50	0.78	0.52	0.41	1.10	0.71	0.80	0.93	0.39	0.17	1.11	0.88	0.55	0.97	0.30
PBD ^2				-1.06	0.89	0.23	-0.88	0.93	0.35	-1.18	0.91	0.20	-0.95	0.92	0.30
PBD (max)										0.53	0.57	0.34	0.65	0.54	0.23
Breeding experience F	1.29	0.87	0.14	1.45	0.96	0.13				1.43	0.97	0.14			
Breeding experience M	-0.43	0.41	0.30	-0.49	0.43	0.25				-0.37	0.42	0.38			
(D) Fledging success															
n56, 29F, 33M, 6Y															
AIC	128.7			129.1			130.7			132.7			204.6		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	0.98	0.25	<0.001	0.95	0.19	<0.001	0.99	0.26	<0.001	0.99	0.27	<0.001	1.20	0.30	<0.001
Territory quality	0.17	0.21	0.41	0.13	0.19	0.50	0.17	0.21	0.41	0.17	0.21	0.41	-0.03	0.15	0.82
Group size	0.46	0.29	0.11	0.43	0.27	0.11	0.45	0.29	0.12	0.45	0.30	0.13	0.01	0.18	0.96
PBD	0.55	0.44	0.22	0.29	0.68	0.67	0.44	0.80	0.58	0.44	0.83	0.59	0.56	0.52	0.28
PBD ^2				0.08	0.82	0.93	0.13	0.87	0.88	0.13	0.89	0.88	-0.17	0.57	0.76
PBD (max)				-0.02	0.23	0.92				0.01	0.26	0.99			
Breeding experience F	-0.24	0.44	0.59				-0.25	0.44	0.57	-0.25	0.48	0.60			
Breeding experience M	0.12	0.36	0.59				0.12	0.36	0.75	-0.11	0.36	0.75			
(E) Annual fledgling production															
B153, 68F, 77M, 10Y															
AIC	495.3			496.6			497.2			502.7			504.1		
Fixed effects	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
Intercept	0.63	0.09	<0.001	0.63	0.09	<0.001	0.63	0.10	<0.001	0.62	0.09	<0.001	0.62	0.09	<0.001
Territory quality	0.08	0.06	0.22	0.08	0.06	0.20	0.08	0.06	0.19	0.07	0.06	0.22	0.07	0.06	0.22
Group size	0.10	0.07	0.14	0.11	0.07	0.13	0.10	0.07	0.15	0.09	0.06	0.13	0.09	0.06	0.13
PBD	-0.10	0.16	0.51	0.02	0.22	0.91	-0.12	0.25	0.65	0.16	0.16	0.36	0.08	0.20	0.68
PBD ^2				-0.15	0.17	0.40	-0.11	0.18	0.53	-0.16	0.17	0.36	-0.13	0.18	0.44
PBD (max)							0.11	0.10	0.24				0.07	0.09	0.46
Breeding experience F	-0.02	0.11	0.86	-0.02	0.11	0.83	-0.04	0.11	0.74						
Breeding experience M	0.12	0.12	0.32	0.13	0.12	0.28	0.17	0.13	0.19						

Table S2. Longer pair bond duration (PBD) was not associated with greater annual likelihood of survival (1/0) for males (M) or females (F). Survival of females was lower age. The last two years of records for each breeder with known pair bond duration were included. Results from a GLM with binomial distribution. Estimates are relative to 1, n = # individuals. P < 0.05 in bold

	Females			Males		
Models	n67			n77		
Fixed effects	Estimate	SE	p	Estimate	SE	p
Intercept	2.7	0.81	<0.001	2.2	1.25	0.08
Fledgling production	0.09	0.27	0.73	0.50	0.33	0.13
Territory quality	0.06	0.28	0.84	0.18	0.32	0.56
Group size	0.34	0.35	0.33	-0.59	0.35	0.09
PBD	0.27	0.81	0.74	-1.72	1.01	0.09
PBD ^2	-0.52	0.75	0.50	1.72	1.10	0.12
Age F	-0.03	0.01	0.08	-0.01	0.02	0.97
Age M						

Figure S1. Number of partners individuals had throughout their lives ($n = 317$ pairs). All pairs in our population included which are, pairs with known and unknown pair bonds (pairs found at original study population in 2005) and incestuous pairs ($n = 29$).



Declaration for Thesis Chapter 4

Declaration by candidate

In the case of Chapter 4, the nature and extent of my contribution to the work was the following:

Nature of contribution	Extent of contribution (%)
The key ideas, data analysis, lab work and writing of the manuscript were my responsibility.	90

The following co-authors contributed to the work. If co-authors are students at Monash University, the extent of their contribution in percentage terms must be stated:

Name	Nature of contribution
Anne Peters	Assistance with writing manuscripts, design of hypotheses, data collection, interpretation of results, feedback on thesis
Michelle L. Hall	Assistance with writing, data collection, interpretation of results.
Sjouke A. Kingma	Assistance with writing, data collection, interpretation of results.
Paul Sunnucks	Assistance with writing, interpretation of results.

The undersigned hereby certify that the above declaration correctly reflects the nature and extent of the candidate's and co-authors' contributions to this work.

Candidate's Signature

Date: 15-10-2016

Main Supervisor's Signature

Date: 15-10-2016

Chapter 4

Incest avoidance, extra-pair paternity and territory quality drive divorce in a year-round territorial bird

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Abstract

Divorce can be an important behavioral strategy to improve fitness. This is particularly relevant for species that are territorial year-round with continuous partnerships, where individuals face constraints on partner choice due to limited vacancies and dispersal opportunities. We tested several hypotheses for divorce in such a species, the cooperatively breeding bird *Malurus coronatus*. Based on nine years of detailed information on dispersal and survival of 317 breeding pairs, we tested if divorce is driven by inbreeding avoidance, by a better partner or territory, or by social variables (number of subordinates and fidelity of partners). We found that divorce is important to escape incest: incestuous pairs were substantially more likely to divorce (64%) than non-incestuous pairs (14%). However, incestuous pair bonds lasted up to a year, highlighting constraints on breeder dispersal. Non-incestuous pairs also divorced, but here the only predictor for divorce was the presence of

extra-pair offspring in a previous brood. Although reproductive failure did not trigger divorce, and reproductive success did not improve in the year following divorce, females that dispersed after divorce obtained higher quality territories, unlike females that dispersed after their partner died. Thus divorce may be a strategy to improve long-term benefits associated with better territories. Some divorces appeared to be forced evictions by older females, although direct evidence for this is limited. Taken together, our findings demonstrate the complexity of factors that affect the occurrence of divorce when partner choice is constrained.

Keywords: breeder dispersal, inbreeding, infidelity, long-term pair bond, monogamy, cooperative breeding

Introduction

In pair-breeding animals, optimal choice of a breeding partner has major fitness benefits (Andersson 1994, Black et al. 1996). Additionally, there is ample evidence that mate familiarity results in higher fitness over time, especially in species that establish long-term monogamous pair-bonds and have bi-parental care (Black et al. 1996, van de Pol et al. 2006). Nonetheless, divorce, the dissolution of a pair bond in which both individuals remain alive and one or both have re-paired, occurs in 92% of socially monogamous birds (Choudhury 1995, Black 1996, Ens et al. 1996, Culina et al. 2014). It is therefore expected that changing social partners and re-mating should be an adaptive decision, with benefits greater than costs (Culina et al. 2014). In species where partners separate between breeding seasons, the benefits of fidelity and the costs of finding a new partner are relatively easily surpassed by the costs of waiting for the former partner who might not return (Ludwig and Becker 2006). However, in species that form year-round pair bonds, there is no uncertainty over the fate of the partner. In such species, re-pairing after divorce requires eviction of another breeder or

opportunistic dispersal into a vacancy created by mortality or dispersal of territory owners (Ens et al. 1993, Dubois et al. 1998). Thus, in such systems, divorce is expected to represent a balance between abandoning a breeding position (i.e. cost), and the relative benefits that are associated with doing so.

Several adaptive hypotheses for causes of divorce have been proposed (reviewed by Choudhury 1995). For species with year-round bonds they can be grouped in three main categories: (a) the 'Better-Option' Hypothesis (Davies 1989, Ens et al. 1993, Desrochers and Magrath 1996) predicts that individuals with low prior breeding success, a low quality partner, or in a low quality territory might move to opportunistically take a better option. This hypothesis predicts that at least one member of the divorced pair will benefit by increasing their reproductive success with a new partner. This could be achieved by obtaining a more compatible or higher quality partner or a better breeding territory. (b) The Inbreeding Avoidance Hypothesis (Koenig and Haydock 1998, Hatchwell et al. 2000, Cockburn et al. 2003) predicts that divorce is more likely when partners are closely related, which is particularly relevant for species with kin-structured populations, in which such pair bonds are relatively common due to inheritance of a breeding position. If so, most likely both, but at least one, members of the pair will re-pair with an unrelated individual after divorce. (c) The Forced-Divorce Hypothesis (Taborsky and Taborsky 1999) predicts that divorce is not initiated by either partner but caused by an intruder that displaces a member of the same sex, and fitness benefits are accrued by the intruder and no improvement will be evident for former pair members after divorce. These hypotheses are not exclusive and multiple mechanisms may occur within one species. Therefore, hypotheses should be considered simultaneously when assessing the underlying causes of divorce (Choudhury 1995).

A recent meta-analysis (Culina et al. 2014) confirmed that divorce is an adaptive strategy to increase reproductive success, rather than an unselected, non-adaptive event or a

by-product of another strategy (Choudhury 1995). This same study also showed that the social and ecological factors driving divorce remain elusive (Culina et al. 2014). A contributing aspect may be that factors driving divorce are often studied independently of factors driving dispersal, yet the two processes are usually inextricably linked. In year-round territorial species, divorce is not just about changing partners, but requires one individual to disperse - with all the associated costs and benefits. Limited understanding of dispersal patterns can lead to a failure to distinguish emigration and mortality, with non-breeding individuals that dispersed to outside the study site assumed dead (Culina et al. 2015). In such cases, the observed divorces are a subset of true divorces. A related limitation frequently encountered is the inability to differentiate between two re-pairing categories: divorced and widowed (Culina et al. 2014). For example, 11 of 16 studies in Culina et al. (2014, Table S1) considered both categories as one: birds that changed partners. However, fitness benefits should be most evident when contrasting re-paired divorced with re-paired widowed individuals (Ens et al. 1993, Culina et al. 2014), to distinguish between the actual outcomes of divorce versus partner change. Moreover, other life-history strategies like mating outside the pair bond (i.e. extra-pair mating) might affect selection pressures to divorce. Extra-pair mating and divorce can be alternative or complementary strategies for mate choice, both with a common target, which is to improve reproductive success (Birkhead and Møller 1992, Cézilly and Nager 1995, Ramsay et al. 2000). Thus, in order to understand the adaptiveness of divorce, studies should consider the incidence of alternative mating strategies, in a species with reliable longitudinal information on survival, post-divorce dispersal and new pairing status. This will allow to differentiate between divorced, widowed and faithful pairs (as in Ens et al. 1993, Dhondt and Adriaensen. 1994, Orell et al. 1994, Jeschke et al. 2007, Culina et al. 2014). Our study of divorce in a species with continuous partnerships and year-round territoriality fulfils these criteria.

Here we investigate factors underlying divorce and its consequences in the purple-crowned fairy-wren (*Malurus coronatus*), a year-round territorial cooperatively breeding passerine. We test which predictions of the major hypotheses for divorce (Table 1) are supported in this species that forms long-term pair bonds, can breed year-round and lives in kin-based social groups in saturated habitats with constraints on pairing opportunities (Kingma et al. 2009). We show that occurrence of divorce cannot be explained by a single hypothesis, and several predictions were supported.

Methods

Study species

A population of *M. coronatus* was monitored at Mornington Wildlife Sanctuary, northwest Australia (17°31'S, 126°6'E) from July 2005 until June 2014. The core study area is located along ~15 km of river length between Annie Creek and the Adcock River. Cooperative groups - a dominant breeding pair accompanied by a variable number of male and female subordinates - defend year-round territories linearly aligned along creeks and rivers in vegetation dominated by *Pandanus aquaticus*, an evergreen palm-like medium-sized tree (Rowell and Russell 1997, Kingma et al. 2009). Only the dominant pair performs duets and reproduces and male and female subordinates can help raise offspring, improving productivity and survival of dominants (Hall and Peters 2008, Kingma et al. 2010). Breeding can occur in every month of the year, with a peak during the wet season (Dec-Mar) and often, but not always, a peak during the dry season (Sep-Oct) (Rowley and Russell 1997, Peters et al. 2013). Although the population-wide incidence of extra-pair paternity (EPP) is only 5%, incestuous pairs have a much higher rate of EPP (46%) compared with 3.3% among non-incestuous pairs (Kingma et al. 2013). Some subordinates might be unrelated to one or both members of the dominant pair (Kingma et al. 2011b), but the majority (> 60%) are retained

offspring, and incestuous pairs result from subordinates inheriting a breeding vacancy after the disappearance of the same-sex breeder (Kingma et al. 2011b). Overall, natal dispersal is female-biased with most subordinate males remaining in their natal territory or moving nearby, while females generally disperse farther; however, some subordinate females also show natal philopatry (Kingma et al. 2010, 2013).

Field data collection

Territory boundaries were recorded from repeated observations of the birds' movements and the location of agonistic interactions between groups. Most boundaries remained stable through the years but occasional shifts were recorded. *Pandanus* cover was quantified as an index of territory quality. Birds do not occupy stretches of river vegetation without *Pandanus* and they depend strongly on this vegetation (51% day-time spent in *Pandanus*, and 95% of nests built in *Pandanus*) (Kingma et al. 2011a). Territories with greater *Pandanus* cover have more subordinates (Kingma et al. 2011a), indicating that these territories are more productive or more attractive for subordinates. Because subordinates increase breeder survival and fledgling recruitment (Kingma et al. 2010), territories with greater *Pandanus* cover thus provide benefits to breeders. Also, higher *Pandanus* cover reduces the likelihood of nest predation, which is the most important source of reproductive failure (Hidalgo Aranzamendi et al. unpubl. data). Thus, we assume that a territory with greater *Pandanus* cover reflect the quality of a breeding territory. *Pandanus* cover was quantified along the territory by one observer assigning a score between 1-10, every 50 m (10 each river side, maximum total 20). An average of all points was calculated for territories longer than 50 m.

Since 2005, all birds in the core study area were individually color-banded and group composition, dispersal and survival documented. Between 2005 and 2010, territories were monitored weekly year-round and all breeding attempts followed. From 2010 onwards, the

population was monitored in two censuses per year: in May-June and in November, following the reproductive peaks. During this period, all new unbanded birds were banded and a blood sample was taken for parentage analysis. All banded birds that survived were resighted and social status (subordinate or dominant) recorded.

From 2007 onwards intensive yearly censuses along the tributaries that join the study site were conducted, to find birds that had dispersed outside the core area (emigrants). These censuses covered almost all suitable habitat within 20 km of the core area, and some up to 60 km away, covering a total of 95 km of river length (including Adcock, Hann, Fitzroy rivers and Throssell, Roy and Spider creeks). To locate birds during these censuses, a 90-second song playback was used at intervals of 100 m or less to attract resident birds. The accuracy of this technique is high, since 90% of dominant birds respond to on-territory playback (Hall and Peters 2008). During these censuses, eight divorced breeders were found (plus 22 other banded birds from the core area). Additionally, no bird from our population was resighted during censuses conducted at a landscape scale in the surrounding potential habitat, and dispersal outside the river vegetation has never been recorded for this species (Skroblin and Legge 2010, Skroblin et al. 2014).

Between 2005 and 2010, no dominants were resighted after being declared dead on the basis of failure to sight them in intensive surveys. After 2010, 3.2% of breeders were initially assumed dead in one census but then found during a subsequent census in a different territory within the core area ($n = 10$ birds). Given that no birds were resighted outside the core area after being declared dead, it can be assumed that very few pair bonds classified as ended by death actually were divorces.

Throughout the study, 317 different breeding pairs were recorded, totaling 507 pair-years (179 dominant males, 192 dominant females). Average group size (breeders plus subordinates) was stable around a mean of 3.6. Annual survival of dominants was on average

81% and average sex-ratio of adults was 1.2 males per female (Kingma et al. 2009). On average, 7.3 (range 6-10) new immigrant females entered the study site per year. Most (70%) of these settled as dominant breeders, totaling 6.9% of immigrant breeders per year of the study period (no. immigrant birds*100/no. breeding adults). The proportion of immigrants did not differ between sampling periods (mean before 2010 = 7.8, mean after 2010 = 8.0 immigrants/year). The number of fledglings detected per year did not differ between the two study periods (mean before 2010 = 0.55 fle/pair/year, mean after 2010 = 0.57 fle/pair/year, t-test $t^2 = -0.18$, $df = 1$, $p = 0.43$)

Data analysis

Pair bond duration and frequency of divorce- Divorce was defined as the failure to maintain a pair bond when both partners were still alive and observed with new social partners and/or in new locations. Annual divorce rate was calculated for July – June by dividing the total number of divorces by the total number of pairs present in that year.

Until 2010, pair-bond duration (PBD) was calculated as the time (days) between the first and last date a pair was seen together. After 2010, the start date of a partnership was estimated as the midpoint date between two censuses when birds were first seen paired and the previous census; the end date of a partnership was estimated as the midpoint date between the last census birds were seen paired and the subsequent census. To assess how accurate our estimates after 2010 were, we recalculated PBD for pairs that started and ended between 2005-2010 using the same methods as 2010-2015, by simulating two censuses per year and assigning midpoint dates as the start and end of the relationships. Following this method, we would have missed 15 relationships that lasted less than six months (5 divorces and 10 deaths), out of the 195 relationships in total (7.7%). The simulated estimates of PBD closely resemble the PBD based on weekly censuses ($r = 0.98$), with a mean difference of 43 days

(median = 38). Considering that the mean PBD for all relationships before 2010 was 370 days (median = 201) we believe that the less intensive sampling after 2010 does not alter our conclusions markedly.

Paternity analysis- DNA was extracted following Barrett et al. (2012). Paternity was assigned using Cervus 3.0.3 (Marshall 1998, Kalinowski et al. 2007). Throughout the study, 1111 individuals were genetically screened by two commercial suppliers using 6 or 9 microsatellites (as in Kingma et al. 2009, 2013). Until 2010, we sampled nestlings and these could be unambiguously assigned genetically to the local breeding female. The sires of EP offspring were identified by repeating the analysis including as possible fathers all dominant and subordinate males present at the time of capture. Less than 5.7% offspring were sired by an extra-pair (EP) father (Kingma et al. 2009, 2013). After 2010, nestlings were no longer sampled and instead we assigned paternity to unbanded birds found at each census (these could be fledglings, subordinates or immigrants). First, all unbanded birds were tested as offspring of the local breeding pair (i.e. the dominant pair of the territory in which they were captured). If the local breeding pair did not match as genetic parents, we tested whether the unbanded birds were subordinates that had already moved from their natal territory; we did this by testing as potential parents all breeding pairs present at the time of capture or last seen in the previous census (i.e. each pair in the population was tested as putative parents to previously unassigned birds). We also tested EP fathers as indicated above. Unbanded birds were considered immigrants if they could not be assigned to the local breeding pair or to other breeding pairs. The two periods with different methods of assigning parentage yielded comparable results: 2011-14, the percentage of EPP remained similar (6.1%) compared to during 2005-2010 (5.7%; Kingma et al. 2013).

Incest and relatedness- Information about the occurrence of incest was extracted from a genetic pedigree containing all known parent-offspring relationships. Twenty-nine socially-

bonded pairs were thus identified as first-degree relatives (mother-son, father-daughter, and brother-sister), and categorized as “incestuous”. One brother-sister pair was excluded from all analyses because they were unfamiliar with one another (hatched in different years and never concurrently resident on their natal territory). All other pairs were categorized as “non-incestuous”; according to the pedigree, five of those pairs consisted of second- and third-degree relatives. In addition, pairwise genetic relatedness of pair members (LR estimator; Lynch and Ritland 1999) was calculated using 6 microsatellites (as in Kingma et al. 2013) with GenAlEx 6.5 (Peakall and Smouse 2012).

Statistical Analyses

Design of analyses

The hypotheses explaining adaptive divorce make several different predictions (see Table 1; adapted from Choudhury 1995). The Inbreeding Avoidance hypothesis predicts that divorce is more likely when partners are related (e.g. incestuous pair, first-order relatives). We define inbreeding avoidance here as avoiding mating with first-order relatives (i.e. incest avoidance, Koenig and Haydock 1998). This hypothesis predicts that one or most likely both partners should show reduced relatedness to their new partner after divorce. The Better Option hypothesis predicts that individuals with low prior breeding success, a low quality partner, or in a low quality territory might move to opportunistically take a better option. The benefits of divorce should be evident in the outcome after divorce for one of the former partners, if they achieve greater reproductive success, obtain a better territory or a better partner than previously. Additionally, divorce can also be associated with infidelity (extra-pair mating). In this case, it is predicted that either females will divorce and subsequently pair with a former EP mate or males will evict unfaithful females. The predictions of the Forced Divorce hypothesis are clear: the only partner characteristics that might be identified as drivers of

divorce would be lower competitive ability than the replacement individual (age, size). After divorce, neither ex-partner is expected to benefit, only the intruder. In this case, previous reproductive success does not affect the probability of divorce, and there is no change in breeding success after divorce.

To test these predictions, (1) we first compared the pattern of pair bond persistence for incestuous and non-incestuous pairs. Divorce affected those two groups differently to such an extent that they could not be analyzed in a single statistical model (all incestuous pairs divorced within a year; see results); so, for all subsequent analyses, incestuous and non-incestuous pairs were analyzed separately. (2) We analyzed the possible drivers of divorce and pair bond duration, and (3) we analyzed the outcomes of divorces to test if divorce led to improvements of breeding success or reduced relatedness to partners in either sex. Finally, we explored if any of the patterns found were consistent with forced divorces.

Samples sizes vary for each analysis due to missing parameters, see Tables for sample sizes and text for details.

1. Pair bond persistence: the importance of incest avoidance

To investigate to what extent inbreeding avoidance is a driver of divorce, we tested whether the probability of divorce depended on the type of relationship (incestuous or not; independent variable) using a survival analysis. This allows inclusion of pairs in which an individual died and persisting pairs at the end of the study (as right-censored cases). This analysis expresses the probability that relationships lasting any given length will be terminated by divorce (Cox 1972, Cockburn et al. 2003). First, the persistence over time of all incestuous and non-incestuous pairs in each of the three classes (divorced, widowed and ongoing) was plotted using Kaplan-Meier graphs with the *survdiff* function of the survival package (Diez 2012). Second, a Cox's proportional hazard analysis was performed comparing pair bond persistence in both groups (using *coxph* in the same package).

2a. Drivers of divorce: What determines the likelihood of pair bond dissolution?

To investigate which factors are drivers of the likelihood of divorce in non-incestuous pairs, we scored for each year of study (July-June) whether pairs present on 1st July of each year were still together or ended in divorce (binomial response variable). This dataset (n = 126 pairs) excluded relationships ending due to death of one of the pair-members, because these could have divorced before death, if both had survived. For this, a GLMM was constructed including male ID and female ID as random factors, to account for multiple entries for males and females that stay together longer than a year or that were in more than one pair over the study. Predictor variables were: genetic relatedness (LR estimator), reproductive success, territory quality and group size; we also controlled for female origin (local/immigrant; all males are residents). Group size (on 1st July of each year) was included, because breeders derive reproductive and survival benefits from living in larger groups (Kingma et al. 2011b). Similarly, a territory of high or low quality could be an asset that influences divorce (see Field Data Collection for details). Reproductive success (number of fledglings, range 0-8) was the number of offspring that survived at least six weeks during the calendar year (July-June). Annual variation in fledgling production is larger (range 16-37 fle/year) than the variation between the two study periods (see Field Data Collection), therefore year was included as a random factor.

We built a second GLMM with the predictor and random variables of the first model adding another predictor variable: whether any previous broods of the pair contained EP offspring (as a proxy of infidelity in the pair). For this analysis, only pairs that reproduced and for which offspring had been genotyped could provide this information, so sample size was much reduced (n = 53 pairs).

Since the number of fledglings produced has a large degree of stochasticity (e.g. nests often fail due to predation and flooding, unpubl. data), this reduces the likelihood of detecting

breeding failure as a driver of divorce (Culina et al. 2014). For this reason, and because birds can use hatching success as an indicator of within-pair compatibility, another model was built using hatching success (proportion of eggs that hatched from each clutch for all nests found in a calendar year) instead of number of fledglings. Hatching success data were available only for 2005-2010, when all nesting attempts were followed in detail. Presence of EP offspring was not included, due to insufficient sample size (we did not know paternity for a large number of nestlings that were depredated or nests flooded before sampling).

Although clutch size and timing of breeding may be important determinants of fitness in general (Culina et al. 2014), we did not test whether these factors affected the likelihood of divorce in *M. coronatus*. Clutch size is extremely consistent (2.93 ± 0.05 SE eggs, unpubl. data) and birds breed year-round, thus the definition of timing of the onset of breeding would be arbitrary and but more importantly, its meaning would be unclear in terms of fitness, as we have no indication that there are distinct seasonal differences in success.

2b. Pair bond duration in divorced pairs

To test if any factor predicted pair bond duration (number of days, log-transformed, dependent variable) for pairs that eventually divorced, we built linear models with genetic relatedness, territory quality and group size as independent variables. We constructed separate models for incestuous and non-incestuous pairs. Genetic relatedness was not included in the model of incestuous pairs. Group size at the start of the pair bond was used to avoid problems distinguishing cause and effect (pairs that were together longer had more time to breed and produce helpers).

3. Outcomes of divorce

Individuals may divorce in order to obtain a less related partner, or a partner of higher quality, and/or, if an individual disperses, better quality of the new territory. Those changes can only be detected by comparing partners and territories (former vs. new) and by

comparing individuals that have experienced partner change: divorcees vs. widows (individuals whose partner died). Three approaches were used to test whether divorce resulted in improvements in partner or territory quality: (i) within-bird comparison between the new partner and the ex-partner (paired comparison) (ii) comparison post-divorce between ex-partners and their new partners (paired comparison) and (iii) comparison of changes in divorcees compared to changes for widows.

Predictor variables were: genetic relatedness, reproductive estimates, age and size of partners, territory quality and group size. For analyses of reproductive estimates, we included the offspring produced during the last year with the ex-partner versus the offspring of the first year with the new partner. Pairs that were together less than 6 months or associated only through the dry season were excluded, since the wet season is the time when most pairs reproduce. Age and size were used as measures of individual quality or competitive ability. Age has been reported as an important factor in divorce for other species (e.g. older partners may be preferred after divorce or older birds may be less likely to divorce; McNamara and Forslund 1996, Green et al. 2004, Cockburn et al. 2008, García-Navas and Sanz 2011). Similarly, size is often regarded as an important signal of quality in small songbirds (Cardoso 2011); larger purple-crowned fairy-wrens males are able to produce lower-pitched low-frequency songs, suggesting that size is important in sexual competition (Hall et al. 2013). Tarsus length (± 0.1 mm) was used as measure of body size. Finally, changes in territory quality and group size are relevant only for individuals that dispersed (i.e. changed territories).

(i) Within-bird comparisons were performed with the difference between the characteristics of the new partner minus the old partner as a dependent variable in mixed models, with bird ID as random factor. There is a significant difference between partners if the intercept in these models differs from zero (Varian-Ramos and Webster 2012). We tested

whether new partners were less related, larger than previous partners or were older (including only birds with known hatch date, age (in months) at the time of divorce vs age of new partner at first date seen together), and if new pairs had higher reproductive success. To test if post-divorce dispersal resulted in the acquisition of a higher quality territory (*Pandanus* cover), or a larger group size, all female dispersers were grouped (incestuous and non-incestuous) and the differences between the old and new (post-divorce) territory were compared, adding bird ID as random factor. For males dispersing post-divorce, a paired t-test (due to low sample size $n = 7$) was used to compare territory quality and group size between the old and new territory. (ii) For post-divorce comparisons between ex-partners and their new partners (divorced female and new partner vs divorced male and new partner), we compared the differences in reproductive output between both new pairs using a GLMM with: (number of fledglings produced by divorced female + new partner) – (number of fledglings produced by divorced male + new partner) as dependent variable and both male and female ID as random terms. No other characteristic was compared between ex-partners and their new relationships, since changes will be determined only by who dispersed or stayed (analyzed in previous section). (iii) We compared changes in divorcees with changes for widows, as a control group, to test costs of partner change. Genetic relatedness and reproductive success of new pairs were compared between divorcees and widows. Similarly, characteristics of new partners (age and size) were compared between divorcees and widows. We used these variables as dependent terms in GLMMs with ML and Poisson distribution or REML models for continuous variables, in which divorce and death were independent variables and bird ID a random factor. Sample sizes for widowed incestuous pairs were small, so we only compared non-incestuous pairs. To test if post-widowhood dispersal resulted in changes in territory quality or group size, we compared the differences between the old and new (post-widowhood) territory, this analysis was restricted to dispersing females (paired t-

test). Information of territory quality for males dispersing post-widowhood was incomplete (n = 5 of 9 males dispersed to outside the area for which we had territory quality estimates), so they were not analyzed.

All analyses were done in R 3.2.0 (R Core Team 2015). A mixed modelling approach (GLMM) was used when data had repeated measures from the same individual(s) (as random term(s)) using the *lmerTest* and *lme4* package (Kuznetsova et al. 2014, Bates et al. 2015). Generalized linear models (GLM) were run first without random terms and quasibinomial distributions to estimate dispersion. All models indicated that data were not overdispersed ($\chi^2 = 1.02$), so GLMMs were appropriate (Quinn and Keogh 2002). R^2 values (Nakagawa and Schielzeth 2013, Johnson 2014) were calculated using the *MuMIn* package (Barton 2014). For models with random terms, individual-level repeatability was calculated following Nakagawa and Schielzeth (2010). Models had values of repeatability close to zero unless reported. For model analyses without random effects, linear models (LM) and t-tests were used. Residuals for models with continuous variables were checked for normality and variables log-transformed if necessary; all independent variables were checked for collinearity (all $r < 0.56$).

Results

Constraints on acquisition of first and subsequent partners

Almost 15% of males and 7% of females acquired their first partner by inheriting the breeding position on their natal territory, and such inheritance generally resulted in the formation of incestuous pairs (detailed information on routes to formation of first and subsequent partners are provided in Table S1 and S2). In total, 28 incestuous pairs formed during our study (first and subsequent partners): 15 males paired with their mother, 6 females

with their father, and 7 pairings were between full siblings. However, most individuals acquired their first partner by natal dispersal: 60% females and 58% males.

Subsequent partners were obtained after a partnership ended in divorce (19% of 317 pairs recorded) or due to the death of one pair member (53% of 317 pairs); the remaining partnerships ended when both partners died, 6%, or were ongoing, 22%. Eleven males and 8 females divorced more than once. The average annual rate of divorce was 8%, fluctuating between 5% and 13%. Divorce occurred in any month of the year, although never when pairs had dependent young.

Individuals that divorced and dispersed obtained an unrelated partner (except one unusual case of pairing between unfamiliar relatives; Table S2). After divorce, in 88% of 50 cases, it was the female that dispersed much more frequently than males (binomial test $p < 0.001$). In contrast to divorcees, the majority of widowed individuals did not disperse (83%) and this was similar for females (61 of 77) and males (78 of 87, binomial test $p = 0.32$). The risk of pairing incestuously for birds that remained as breeder in the territory following divorce or widowhood was higher for females (25% of 67) compared to males (8% of 119; $\chi^2 = 9.88$, $df = 1$, $p = 0.001$).

Divorce in incestuous pairs

Divorce occurred more often in pairs formed by first-order relatives (incestuous: 64% of 28) compared with non-incestuous pairs (14% of 285) (Cox PH $\chi^2 = 18.50$, $df = 1$, $p < 0.001$, Fig. 1). All incestuous pairs divorced ($n = 18$, median = 107, range 7-364 days) or ended by partner death ($n = 10$, median = 60, range 29-188 days) within a year. The duration of incestuous pair bonds was not explained by territory quality ($R^2 = 0.21$, $F_{2,16} = 2.09$, $z = 0.05 \pm 0.06$, $p = 0.43$), and although incestuous pairs in larger groups tended to stay together

longer than pairs in smaller groups, the effect size was small ($z = 0.34 \pm 0.17$, $t = 1.97$, $p = 0.06$).

Divorce in non-incestuous pairs

One driver of the likelihood of divorce was identified: non-incestuous pairs that previously had EP offspring had a higher likelihood of divorce ($z = 2.56 \pm 1.11$, $p = 0.02$, Table 2). EP offspring occurred in 21% of divorcing pairs (3 of 14 reproducing pairs, Fig. 2) compared to 8% in pairs that did not divorce (3 of 39, Fig. 2). Neither genetic relatedness between partners nor previous reproductive success predicted whether pairs divorced (Table 2). Pair bond duration for non-incestuous pairs that divorced was extremely variable, and sometimes very long ($n = 40$, median = 224 days, range 7-1824, Fig.1). However, no variable predicted pair bond duration ($R^2 = 0.24$, $F_{3,26} = 2.67$, group size $z = 0.30 \pm 0.17$, $t = 1.72$, $p = 0.10$, territory quality $z = 0.07 \pm 0.05$, $p = 0.18$, and relatedness $z = 2.70 \pm 2.10$, $p = 0.21$).

Outcomes of divorce

When incestuous pairs divorced, both pair-members subsequently paired with a less related individual (LR estimator for females: $x = -0.50$, males: $x = -0.54$, both $p = 0.01$, Table 3). Genetic relatedness between the bird that dispersed and the new partner were not different from the average genetic relatedness between the same dispersing bird and any other dominant bird of the opposite sex in the population (paired t-test for divorced females that dispersed, $n = 15$, $t = -0.09 \pm 0.01$, $df = 10$, $p = 0.47$). For non-incestuous birds, there was no evidence of an effect of divorce on the genetic relatedness with their new partner (Table 3, females $t = 0.02$, $df = 31.99$, $p = 0.59$; males $t = -0.03$, $df = 26.74$, $p = 0.33$). No improvement in reproductive success followed divorce in either incestuous or non-incestuous pairs (Table 3). Males that were divorced by a non-incestuous partner ended up with a partner that was older than the previous one ($x = 17$ months older; $df = 9.95$, $p = 0.02$, Table 3). No other

partner quality attributes differed before and after divorce (Table 3). Annual reproductive success of divorcees with their new partners was not significantly different between the sexes ($n = 45$ pairs, $x = 0.57 \pm 0.98$ and 0.27 ± 0.65 fledgling/year for female and male respectively, $z = 0.41$, $df = 32.90$, $p = 0.07$), regardless of whether females or males stayed.

On average, females dispersing after divorce moved to territories with more *Pandanus* cover (i.e. to a higher quality territory; $n = 44$, $t = 2.20 \pm 1.06$, $df = 34$, $p = 0.01$; Fig.3), but males did not ($n = 7$, $x = -3.00$, $p = 0.98$). For both sexes, post-divorce dispersal did not lead to a change in group size and the direction of the effect was opposite from expected (i.e. individuals moved to smaller groups; females $x = -1.43$, $df = 34$, $p = 0.26$; males $x = -2.25$, $p = 0.10$). For three divorcing females, we observed fights between the replacing and the dispersing female, followed by the intruder female taking over the breeding position. The replacing females were an older dominant female, an immigrant of unknown age and a subordinate female and all of those three females were in neighboring territories before usurping the dominant position. Afterwards, the evicted females were observed floating through several territories before taking new breeding positions. All three evicted females moved to an inferior territory, with lower *Pandanus* cover. More generally, when divorcing females moved to an inferior territory after divorce (an indication that they may have been evicted), 67% of the ex-partners (10 of 15) were joined by an older female. In contrast, when divorcing females moved to a better territory, 30% of the divorced males (8 of 27) obtained an older female, which is significantly less often ($8/27$ vs $10/15$, $\chi^2 = 5.40$, $df = 1$, $p = 0.02$). On average, the time to obtain a new breeding position after divorce was longer for females that moved to lower-quality territories ($n = 8$, median = 42 days) than for females that moved to higher-quality territories ($n = 12$, median = 6 days, data from 2005-2010 only), although those differences were not significant (t-test of log-transformed days to re-pair after divorce, $t = -1.76$, $df = 18$, $p = 0.09$). Widowed females that dispersed did not obtain territories of better

quality (Fig.3, paired t-test, $n = 13$, $x = -0.38$, $df = 12$, $p = 0.24$), or experience a change in group size ($x = -0.83$, $df = 12$, $p = 0.28$). No other characteristic was different when comparing divorcees and widows (Table S3).

Discussion

We found support for several hypotheses for divorce in cooperatively breeding *M. coronatus* (Table 1). The Inbreeding Avoidance hypothesis was supported by the observation of high rates of divorce among incestuous pairs and that those individuals paired with less related partners after divorce. The Better Option hypothesis was supported by evidence that dispersing females obtained higher quality territories following divorce. We also directly observed a few evictions of breeding females by a usurper and some further indirect support for the Forced Divorce hypothesis. Finally, we found that the occurrence of infidelity (EPP) was a predictor of divorce, although its meaning is unclear in terms of long-term fitness for either sex.

Divorce to escape inbreeding in incestuous pairs

Divorce in *M. coronatus* is an important mechanism to escape incest (Fig.1). Incestuous pairs frequently resulted when birds did not disperse from their natal or breeding territories (Tables S1 and S2), suggesting constraints on opportunities for dominant and subordinate birds dispersing to a breeding position. In line with this, many incestuous pairs persisted for a substantial amount of time (average = 107 days, max = 1 year). Since males are more philopatric than females, mother-son pairings were the most common form of incestuous pairs, and the risk of engaging in an incestuous relationship following death or dispersal of a partner was three times greater for females (25% females vs 8% males). Females usually dispersed after divorce, but were less likely to disperse after death of a partner (Table S2),

despite the high risk of incest. This lack of breeder dispersal after an unexpected event, such as partner death, implies that divorce in *M. coronatus* is usually an opportunistic stay-and-wait strategy, and breeder dispersal is triggered when a more attractive vacancy is created elsewhere by the death or divorce of a breeder.

Incest is costly for females but even more so for males: incestuous pairs have a 30% reduction in hatching success, and almost 37.5% of the surviving hatchlings are sired by an EP male (compared to 3.3% EPP in non-incestuous pairs, Kingma et al. 2013). Nonetheless, it was usually females that dispersed: 15/17 incestuously paired females dispersed. The fact that many incestuous pairings did not dissolve immediately (see above) suggests that females moved voluntarily, rather than being coerced or evicted by the male: if males were evicting an incestuous partner, given their low expectations of reproductive success (low hatching success and high EPP), we would have expected eviction to occur more rapidly.

Divorce driven by incest avoidance is not uncommon in cooperative breeders, as they are usually constrained by a social environment with a high density of relatives (Koenig and Haydock 1998, Daniels and Walters 2000, Hatchwell et al. 2000, Cockburn et al. 2003). In our study, divorce is a straightforward solution to end incest, and its outcome benefits both members: males and females paired with a less related individuals after divorce (Table 3). However, we found no evidence that dispersers actively sought unrelated partners, since the degree of relatedness among newly formed pairs could have been generated by random mating.

Divorce and EPP: infidelity in non-incestuous pairs

Despite the apparent difficulties of changing breeding partners, divorce was not restricted to incestuous pairs. However, in non-incestuous pairs, genetic relatedness did not predict divorce. Rather, divorce was related to female infidelity: 21% of divorcing pairs had EPP in a

previous brood compared to 8% in non-divorcing pairs (Fig. 2). The link between divorce and previous occurrence of EPP in non-incestuous pairs might reflect two alternative scenarios: EP mating is used to prospect for future partners (i.e. looking for a better quality partner) (Spoon et al. 2007, Pérez-Staples et al. 2013) or it reflects weak pair bonds (Forstmeier et al. 2014). Our available evidence provides no support for EP mating as a prospecting mechanism for a partner of better quality: only one EP father (out of 14) became the new partner after a divorce. In this instance, a female left a son and paired with a previous EP partner who was paired to his daughter until then. We suggest that the positive association between divorce and EP paternity indicates that divorce and EP mating serve – at least to some extent – the same purpose. This relationship reflects the intense limitations on social partner choice (Cézilly and Nager 1995, Ramsay et al. 2000), whereby EP mating is an interim solution for females to compensate for a suboptimal partnership until this can be rectified by acquiring a new social partner through divorce (as in Ramsay et al. 2000).

Reproductive success is not a driver or outcome of divorce

We expected divorce to lead to an increase in reproductive success, or to occur as a response to reproductive failure (Ens et al. 1993, Dhondt and Adriaensen 1994, Black et al. 1996, Culina et al. 2014). However, divorce in non-incestuous pairs of *M. coronatus* is not obviously driven by reproductive failure: neither number of fledglings nor hatching success predicted divorce (Table 2). Similarly, there was no change in reproductive success after divorce (Table 3). More importantly, divorcees did not obtain higher reproductive success compared to individuals that had changed partner due to partner death (Table S3). These patterns could be due to the fact that fairy-wrens are fairly long-lived (Cockburn et al. 2003): improvements in reproduction for species with long-term permanent pair bonds often occur slowly with pair bond duration, as a consequence of mate familiarity or breeding experience (Marzluff and Balda 1992, Cézilly et al. 2000, Van de Pol et al. 2006, Sánchez-Macouzet et

al. 2014). Thus, benefits of divorce might become evident only after multiple breeding attempts: indeed, more generally, reproductive benefits of divorce in long-lived species are less evident (Culina et al. 2014). Additionally, environmental stochasticity (Culina et al. 2014), the proposed main explanation for why performance at later breeding stages does not predict divorce, could apply to breeding success as a whole for *M. coronatus*. Reproductive success for this species is largely determined by predation and flooding events (unpubl. data), as for many tropical species (Martin 2015). Such high environmental stochasticity reduces the potential for reproductive failure to be selected for as a driver of divorce, as well as hampering detection of reproductive failure driving individual divorce decisions. Alternatively, divorce might function as a mechanism to obtain long-term benefits, rather than an immediate reproductive benefit, as we will discuss below.

Improvement after divorce: territory quality over partner quality?

Divorced females that dispersed usually obtained a territory of higher quality. This was independent of whether females divorced a related or unrelated partner or other potential benefits such as number of subordinates on the territory. Such an improvement in territory quality did not occur in dispersing widowed females (Fig. 3) indicating that obtaining a better quality territory is a clear benefit associated with divorce rather than breeder dispersal *per se*. The timing of such divorces was most likely opportunistic, with dominant females seizing an opportunity to obtain a better breeding territory. This seems to be an important female strategy as a third of female breeding vacancies (41/119, Table S2) were filled by another dominant female dispersing, despite the constant presence of subordinate females in the population. The quality of territories has long-term importance for species with site fidelity (Desrochers and Magrath 1996, Heg et al. 2003). This is especially true for *M. coronatus*, in which territories are defended year-round (Hall and Peters 2008) and breeding vacancies

occur rarely. Furthermore, higher quality territories are associated with long-term benefits, because they experience greater nest success (unpubl. data) and support larger social groups, with more subordinate helpers (Kingma et al. 2011a), and helpers over time have a positive effect on fledgling production and breeder' survival (Kingma et al. 2010). Although divorcing females did not immediately acquire a larger group –presumably because subordinates often disperse immediately after death of a related dominant (unpublished data) - in the long run a high quality territory is important for reproductive success. Therefore, in species with site fidelity, territory quality could take priority over partner quality, and divorce could be considered indicative of territory choice rather than partner choice (Ens et al. 1993, Desrochers and Magrath 1996).

Divorce: mostly a female-driven strategy?

In agreement with comparative evidence (Culina et al. 2014), our evidence shows that females benefit more from divorce. First, most commonly the female instigated divorce by leaving (88% of divorces, Table S2) and this was beneficial: divorcees that did not disperse were likely to end up in an incestuous partnership with a resident, former subordinate male (Table S1). Moreover, females dispersing after divorce acquired a higher quality territory (Fig. 3), but no male dispersed to a better territory ($n = 7$, $x = -3.00$, $p = 0.98$). Additionally, some divorces may have been triggered by female-female competition (i.e. forced divorce; Taborsky and Taborsky 1999, Jeschke et al. 2007), driven by older females evicting younger ones. Direct evidence for this hypothesis is limited: we observed that three divorces were preceded by fights with a usurper female, and afterwards the evicted females dispersed to lower quality territories. More broadly, we found that those females that dispersed to a lower-quality territory after divorce took longer to re-pair and were more likely to be replaced by an older female than females dispersing to higher-quality territories (Table 3). Nevertheless, we

cannot discard the possibility that such patterns reflect an undetected process of partner choice by males accepting older females.

Conclusion

We found that several non-exclusive hypotheses simultaneously explained divorce in this tropical cooperative breeder (Table 1). By adding demographic covariates and differentiating pairs according to their degree of relatedness, we found that divorce is a strategy to escape inbreeding for incestuous pairs. For unrelated pairs, previous female infidelity (presence of EP paternity) predicted divorce even though this was not directly linked to future pairing with the EP sire. Additionally, females appear to use divorce as a strategy to acquire a better quality territory. The importance of the acquisition of a better quality territory is in agreement with the absence of immediate improvements in reproductive success, and the species' slow life-history: annual survival is high, annual reproductive success is generally low with a large stochastic component, and the benefits of a good territory are expected to accrue slowly over the long-term. Our detailed longitudinal data and reliable information on survival and movement of all breeders allowed us to overcome the most common limitations that hamper the understanding of divorce (see introduction). Our study provides a clear illustration of the complexity of factors underlying divorce for species with continuous partnerships and year-round territoriality.

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Data Accessibility

Analyses reported in this article can be reproduced using the data provided by Hidalgo Aranzamendi et al. (2016).

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Table 1: Overview of main hypotheses proposed to explain divorce in year-round territorial species with continuous partnerships, and their support in *Malurus coronatus*

Hypothesis	Assumption	Predicted drivers of divorce	Support in <i>M. coronatus</i>	Predicted outcomes of divorce	Support in <i>M. coronatus</i>
Better Option ^{a,b}	Divorce occurs when one member is able to obtain a better partner or territory	Low breeding success	No (for non-incestuous pairs)	Improved reproductive success for one of the former members of a pair	No
		High within-pair relatedness	No (for non-incestuous pairs)	Improvement of genetic relatedness for both ex-partners after repairing	No
		Inferior territory or partner	No – territory quality No – group size	The dispersing pair member obtains: -better territory - larger group One of the ex-partners finds a partner of higher quality	Yes No No ^f
Inbreeding Avoidance ^c	Partners divorce and one disperses to avoid breeding with philopatric offspring	Incest	Yes (for incestuous pairs)	Improvement of genetic relatedness for both ex-partners after repairing	Yes
				Improvement of reproductive success for both ex-partners	No
Forced Divorce ^d	Divorce caused by intrusion of a third individual	Traits of third individual (new partner)	Some evidence for eviction by older females ^g	Intruder benefits Evicted bird suffers	No Some evidence, some females obtain worse territories
Alternative mating strategy ^e	Infidelity associated with divorce	Extra-pair paternity (EPP)	Yes (for non-incestuous pairs)	Female pairs with EP father Males evicts unfaithful female	No No

^aSee also Choudhury (1995) for detailed descriptions of hypotheses and other hypotheses with overlapping assumptions or not applicable to year-round territorial species with continuous partnerships. ^bDavies 1989, Ens 1993, and Magrath 1996 ^cKoenig and Haydock 1998, Hatchwell et al. 2000, Cockburn et al. 2003 ^dTaborsky and Taborsky 1999, ^eBirkhead and Møller 1992. ^fMales re-pairing with an older female is presumed indication of eviction of the ex-partner by new female, since males do not disperse to mate with an older female. ^gDefinitive evidence requires direct behavioral observations of the process of divorce

Table 2: Drivers of divorce in non-incestuous pairs: effects of incompatibility (relatedness), reproductive success (number of fledglings, hatching success), previous extra-pair offspring, group size and territory quality, on the probability of divorce (binomial GLMMs; controlling for female origin). Model (a) test whether number of fledglings predicted the probability of divorce, including pairs that were never successful (n = 126 pairs, 220 observations) and; Model (b) test whether number of fledglings predicted the probability of divorce and included only pairs that produced at least one genotyped offspring so that information on extra-pair paternity (EPP) was available (n = 53 pairs, 81 observations); model (c) tests whether reduced hatching success predicted the probability of divorce, and included only pairs for which hatching success data was available (n = 24 pairs, 44 observations). Random effects did not contribute to the variance explained by the models.

Explanatory variables	(a)			(b)			(c)		
	Estimate	se	z value	Estimate	se	z value	Estimate	se	z value
Within-pair relatedness (LR estimator)	2.03	2.51	0.81	4.97	5.03	0.99	3.54	4.84	0.73
Number of fledglings	0.01	0.19	0.03	0.11	0.23	0.48	n.a.	-	-
Hatching success	n.a.	-	-	n.a.	-	-	-1.99	1.47	-1.35
Extra-pair offspring (y/n)	n.a.	-	-	2.56	1.11	2.30*	n.a.	-	-
Group size	-0.03	0.18	-0.18	0.20	0.21	0.96	-0.10	0.18	-0.55
Territory quality	-0.01	0.06	-0.19	0.05	0.11	0.44	0.08	0.08	0.96
Female origin (immigrant y/n)	-1.58	0.90	-1.76	-1.09	1.21	-0.90	n.a.	-	-

*p < 0.05

n.a. = term not fitted in this model

Table 3: Paired comparisons between the new partner and the partner before divorce (within-bird comparison) to analyze whether divorce resulted in an improvement for divorced females and males. Shown are mean of the change from former to subsequent partners of divorced individuals and p-values for (a) incestuous and (b) non-incestuous pairs. Positive values indicate improvement after divorce; the opposite is true for genetic relatedness. GLMMs for variables with more than one entry per individual, random effects did not contribute to the variance explained by the model, n = number of individuals.

(a) incestuous	Females			Males		
	n	Mean	p	n	Mean	p
Genetic relatedness ^a	13	-0.50	0.01	13	-0.54	0.01
Reproductive success ^{a,c}	7	0.28	0.20	7	0.31	0.17
Partner age (months) ^{a,d}	6	11.43	0.31	6	6.28	0.99
Partner size (tarsus length, mm) ^b	13	-0.43	0.29	10	0.08	0.81

(b) non-incestuous	Females				Males			
	n	Mean	SE	p	n	Mean	SE	p
Genetic relatedness	26	0.02	0.04	0.59	28	0.01	0.03	0.33
Reproductive success ^{a,c}	12	0.09	-	0.31	14	1.00	-	0.34
Partner age (months) ^d	15	3.31	5.14	0.53	11	13.25	4.90	0.02
Partner size (tarsus length, mm)	27	-0.18	0.14	0.35	26	-0.15	0.21	0.41

^a Wilcoxon test or ^bt-tests for variables with reduced sample size

^c Reproductive success is number of fledglings of the first year with the new partner minus number of fledglings produced during the last year with the previous partner

^d only birds with known hatch date

Figure 1. Pairs of first-degree relatives (incestuous) ($n = 28$) divorced more often and had shorter pair bonds than non-incestuous pairs ($n = 285$) ($\chi^2 = 18.50$, $df = 1$, $p < 0.001$). Shown is the probability that the pair bond is ongoing; vertical lines indicate pair bonds ending due to deaths; each step down indicates a divorce.

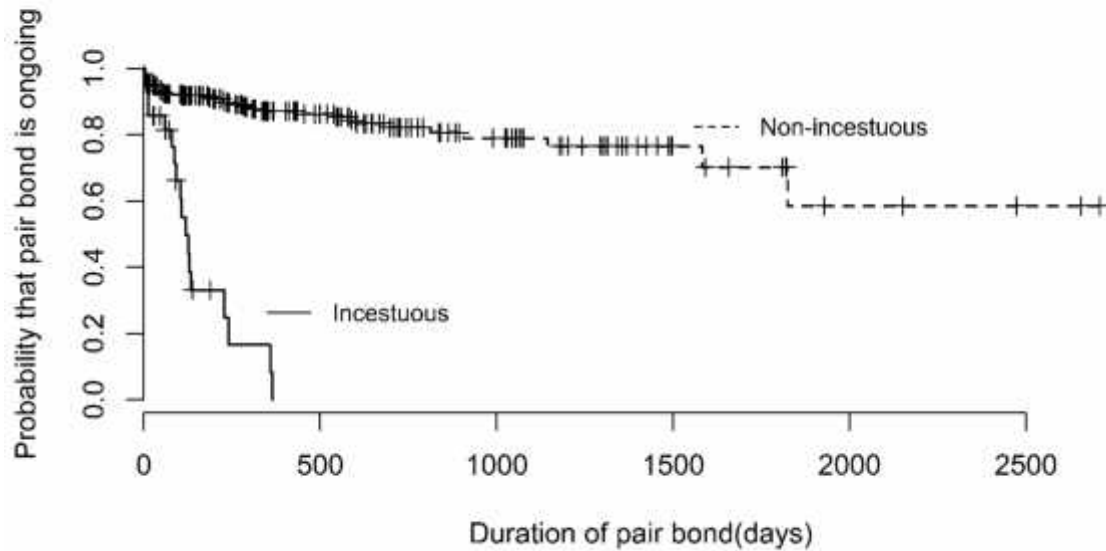


Figure 2. Pairs that divorced were more likely to have had extra-pair paternity (EPP) in previous broods compared to pairs in which one or both partners died, or ongoing relationships ($z = 2.56 \pm 1.11$, $p = 0.02$). Bars show percentage of pairs with at least one extra-pair offspring in previous broods; numbers indicate sample size (total number of pairs, non-incestuous pairs only).

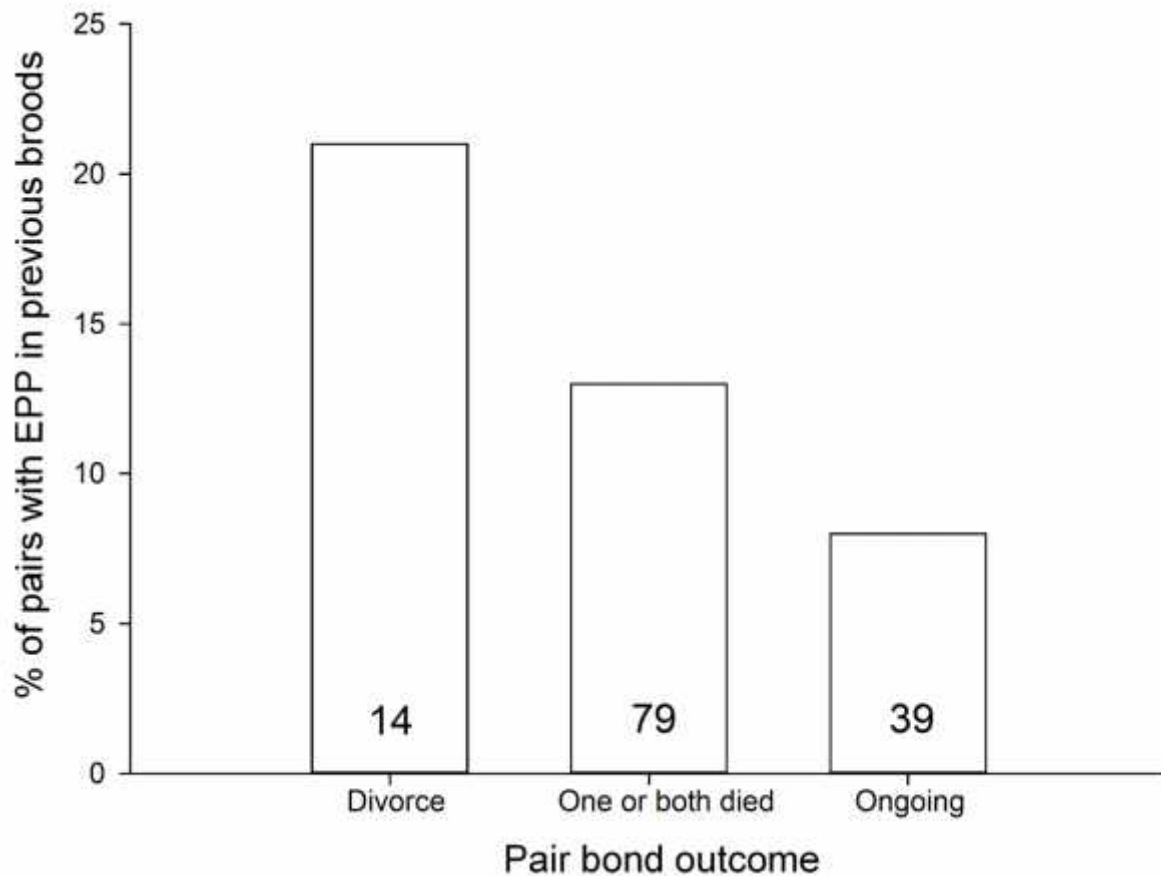
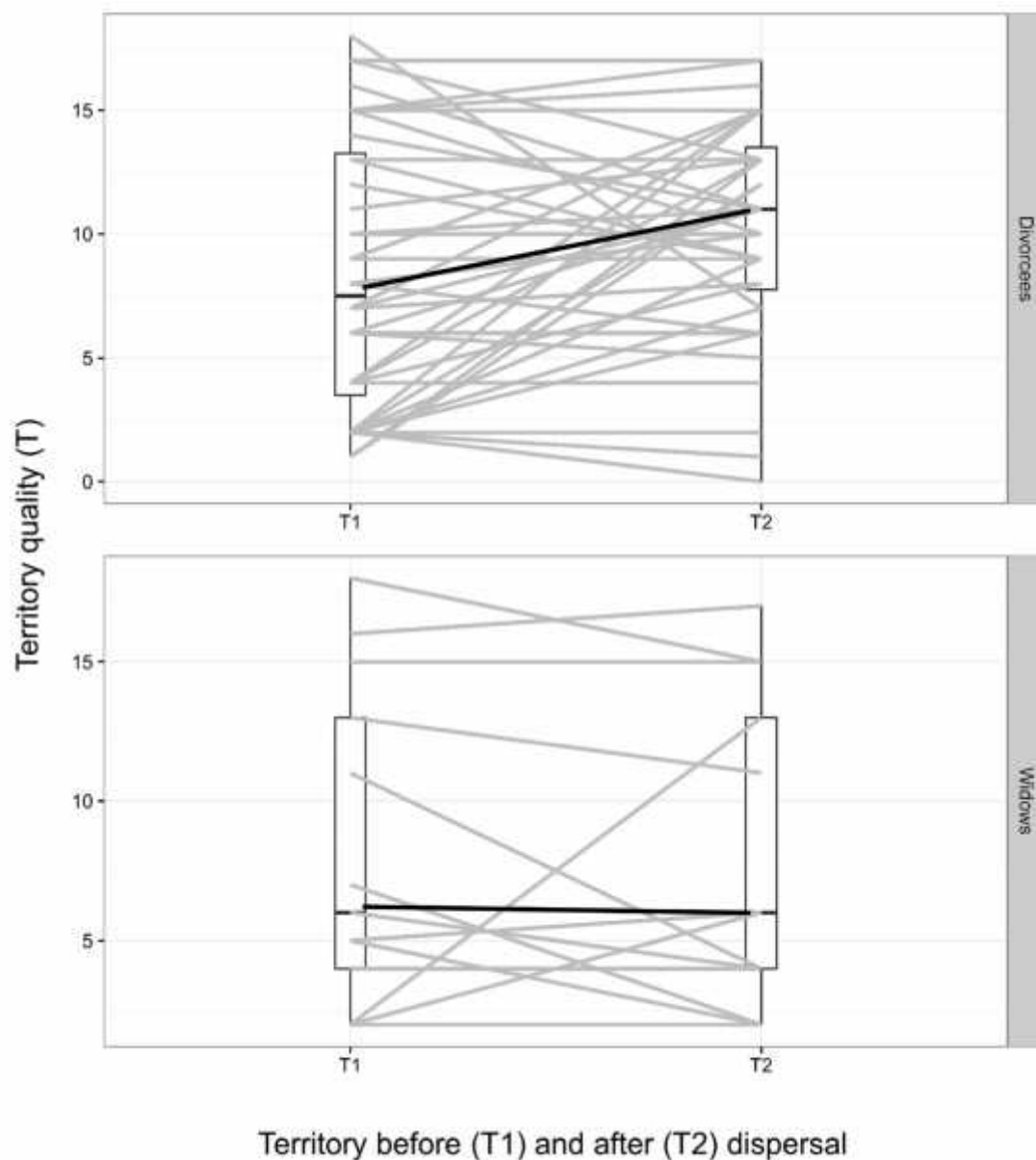


Figure 3. On average, females that dispersed after divorce (panel (a); $n = 44$) moved to better quality territories (T2) than their initial territory (T1; $x = 2.20$, $p = 0.01$). This contrasts with widowed females that dispersed (panel (b); $n = 13$): these did not obtain a better territory ($x = -0.38$, $p = 0.24$). Territory quality is expressed as an index of *Pandanus aquaticus* cover (1-20). Grey lines connect T1 and T2 for individual females, black lines connect medians. Box plots showing the interquartile range (box), medians and SE.



Supplementary Material

Table S1: Most females (90% of 142) acquired their first partner by dispersal within or immigrating from outside the study area, while most males (80% of 132) acquired their first partner primarily on or within 2 territories of their natal territory.

Acquisition of first partner	Females			Males		
	Incestuous	Non-incestuous	Total	Incestuous	Non-incestuous	Total
Inheritance	10	2	12	20	12	32
Fission - Subordinate budded part of natal territory	0	2	2	0	14	14
Local dispersal (1-2 territories distance)	0	11	11	0	60	60
Dispersal > 2 territories (0.1-6 Km)	0	74	74	0	17	17
Immigrant from outside study area	0	43	43	0	9	9

Table S2: Females are more likely to disperse after divorce than are males. Individuals that dispersed after divorce or partner-loss usually acquired unrelated partners. Individuals that stayed in the territory were more likely to form an incestuous pair bond.

Acquisition of subsequent partners		Dominance taken by	New partner for males		New partner for females	
			Incestuous	Non-incestuous	Incestuous	Non-incestuous
After divorce	Stayed (n = 50)	Subordinate within group	6	5	3	0
		Neighbour subordinate	0	15	0	3
		Neighbour dominant	0	16	0	0
		Immigrant	0	2	0	0
	Dispersed (n = 50)*		0	6	1 [#]	43
		Total individuals	6	44	4	46
After death of partner	Stayed (n = 136)	Subordinate within group	2	3	11	6
		Neighbour subordinate	1	27	3	25
		Neighbour dominant	0	25	0	14
		Immigrant	0	14	0	0
		Merged/fission/demoted	0	3	0	2
	Dispersed (n = 28)		1	11	0	16
		Total individuals	4	83	14	63

* In 5 pairs male and female dispersed, 1 pair divided the territory and in 2 cases a female and a male were demoted, not included. [#] One female divorcing her father dispersed 15 km and paired with her brother that dispersed before she hatched.

Table S3: Comparison of partners after partner change depending on whether the partnership ends due to death (widows) or divorce in non-incestuous pairs. GLMM by maximum likelihood used to compare divorced relative to widowed birds; positive means/estimates indicate higher values for divorcees. Random effects did not contribute to the variance explained by the model.

(b) non-incestuous	Females						Males					
	Widows	Divorcees	Mean	Estimate	SE	p	Widows	Divorcees	Mean	Estimate	SE	p
Genetic relatedness	45	22	-0.01	-0.03	0.05	0.87	56	24	-0.01	-0.01	0.04	0.87
Reproductive success ^a	45	18	0.22	0.22	0.40	0.58	57	18	0.04	0.04	0.43	0.92
Partner age	42	22	6.88	6.49	3.56	0.07	36	17	-0.04	-0.04	3.20	0.98
Partner size ^b	45	22	0.01	0.01	0.14	0.92	53	23	0.02	0.02	0.15	0.86

^a Reproductive success included offspring produced during the first year with the new partner

^b Partner size estimated from tarsus length

General discussion

Tropical birds generally have a slow development and start reproducing relatively late in life (Martin 1996, Wikelski et al. 2003, Møller, et al. 2007). Data on ecological drivers of life-history characteristics typical of a slow pace-of-life, have been gathered from a few tropical species that have been studied in detail (Martin 1996, Stutchbury and Morton 2001). This is despite the fact that the tropics have the highest bird richness and biodiversity (Stutchbury and Morton 2001). Developing a wide-ranging theory to understand the slow pace-of-life strategy is particularly urgent in the face of the rapid changes occurring worldwide, since tropical species appear to be highly sensitive to human impacts (Sekercioglu et al. 2012, Chambers et al. 2013). In order to generate this wide-ranging theory, including more information on tropical birds is necessary.

The basic characteristics of life-history (e.g. age at first reproduction, reproductive lifespan and ageing, number and size of offspring) determine a species position within the fast-slow life-history continuum (Ghalambor and Martin 2001, Bielby et al. 2007). One of the most commonly used approaches is to use single traits as indicator variables (Bielby et al. 2007), such as reproduction. Several measures of reproductive performance over the lifetime of individuals can show differential allocation of resources by individuals and the effects that social and environmental parameters exert on shaping reproductive success and thereby life-history (van de Pol 2006).

In my PhD research, I focussed on a central trait of life-history: reproduction. My model species, the purple crowned fairy-wren, is a cooperative breeder that has long periods of parental care, high annual survival, limited natal dispersal and pervasive constraints on mate choice (i.e. highly saturated environment, limited turnover rates of breeding vacancies

and low extra-pair paternity) (Hall and Peters 2009, Kingma et al. 2009, 2010, 2013, Hidalgo Aranzamendi et al. 2016). In my thesis I tried to understand how individual decisions affected reproduction and how their social environment not only contributed information on selective pressures operating within a slow pace-of-life strategy, but also to the preservation and future management of this endangered bird.

Several ecological factors were relevant for reproduction of purple-crowned fairy-wrens. Food abundance driven by seasonality of rainfall is fundamental to determine the breeding cycle of this species but also the survival of offspring. High rates of nest predation are a major driver of nest failure and the large effects of highly variable climate drivers stress the stochastic nature of reproduction in this tropical species. Family groups are essential social factors that brought key benefits for survival of offspring and successful reproduction. Finally, territories located in high quality habitats consistently affect reproductive success and individual strategies. Next, I discuss the main findings of my thesis in detail.

Using recently developed methods that can deal with complex data of multi-brooded species, I demonstrate that female purple-crowned fairy-wrens have a fine-tuned mechanism to time breeding cycles after rainfall and that rainfall simultaneously determines food abundance, such that breeding and food peaks are quite well matched (Fig. 1, Chapter 1). In addition to rainfall determining timing of reproduction, quantity of rainfall prior to egg-laying has a quantitative influence on reproductive output increasing clutch size and number of fledglings, although it has no effect in the nestling condition (Fig. 3, Chapter 1).

The data obtained for purple-crowned fairy-wrens reinforces the idea that more, and more detailed, records of food availability from different tropical environments are needed, in

order to better understand patterns of breeding for most tropical species (Grant et al. 2000, Sekercioglu et al. 2012). This information is urgent because it would provide information if climate-change induced mismatches between food availability and offspring production are occurring at tropical latitudes, similar to those described for northern hemisphere insectivores (Visser and Holleman 2001, Visser et al. 2006a, 2006b, Schaper et al. 2012). Recent evidence has highlighted that such phenological mismatches might be occurring in some southern hemisphere ecosystems (Brown and Shine 2006, Chambers et al. 2013). Moreover, rainfall was identified as the only driver of phenology for this species, and this cue might be relevant in a similar way for many other tropical species (Skutch 1985). Unfortunately, this leaves an important gap of information, since most current identified mismatches between birds' reproduction and food availability are focussed on temperature changes and global warming. Furthermore, predictions for changes in rainfall have not been accurately modelled at a local scale (Chambers et al. 2013), and it is likely that this needs to be solved first, in order to predict shifts or mismatches of food availability and rainfall with high accuracy.

Rainfall is identified as an environmental pressure driving certain characteristics of life-history of purple-crowned fairy-wrens, as their timing of nesting attempts and quantitative output. My analysis highlights that means and extremes of rainfall and temperature have intricate, partly opposing effects that affect reproductive success through multiple processes: nest inundation, predation, egg hatchability and offspring survival (Fig. 1, Chapter 2). Climate variables have sometimes antagonistic effects on the vulnerability of nests and fledglings; for instance, variation not only affect success directly (e.g. reducing viability of eggs and fledgling survival) but indirectly, presumably through effects on

trophic interactions (i.e. predator activity) (Chapter 2). A central result here is the importance of habitat quality, in which more vegetation cover is linked to increased reproductive success (Fig. 1, Chapter 2). These results highlight the level of information required before effects of climate change on populations can be accurately predicted. More importantly, by analyzing effects at each reproductive step, losses are quantified at a finer scale (Fig. 1, Chapter 2) and I was able to identify which environmental selective force is relevant at which reproductive stage. Besides the impact that these complexity might have in the future of this species, it is evident that the likelihood of nest failure at each nest attempt is high. Therefore, it is likely that pairs would try to optimize their reproductive output over long temporal scales, throughout their lifetime. Here, two mechanisms might be key: having multiple broods or investing in long-term partnerships (Black 2001, Oppel et al. 2013).

One way of improving reproductive success is by fine-tuning effective behaviours against nest losses by predation. This could be achieved maintaining long-term relationships with the same partner, if such partnerships are strategic to improve nest defence and brood caring (Black 1996). Despite purple-crowned fairy-wrens having the characteristics that would fit those predictions - year-round long-term pair bonds, almost exclusive social and genetic partnerships and high rates of nest failure - I identify limited benefits from retaining the same partner (Chapter 3). Although the probability of nest failure decreases over the first years with the same partner, no further benefits are detected nor is this translated into recruitment of more fledglings (Tables 1 and 2, Chapter 3). Instead, pairs that stay together less long have lower hatching success. This is possibly due to decreased survival of low-quality females (Chapter 3). As a result of these findings I hypothesize that long-term

relationships could be a by-product of site fidelity and lack of vacancies. In fact, my results show that both forces operate since short to medium-length relationships were associated with high quality territories. Apparently, in lower quality territories, pair bonds end quite soon, or low-quality pairs remain together very long due to lack of individual competitiveness to obtain territories of higher quality. For instance, the high relative occurrence of incestuous pairs (9% of partnerships, 3.5% of total pair bond time), despite high costs of incest, are clear indicators that purple-crowned fairy-wrens face strong constraints in availability of breeding vacancies that characterise cooperatively breeding species in general (Cockburn 1998, Hatchwell and Komdeur 2000, Koenig and Dickinson 2004). Site fidelity of pair members could be then reinforced in this species by the high value of good territories. Territories with higher vegetation cover are key in reducing the likelihood of nest predation (Chapter 2) and recruit more fledglings, highlighting the importance of good assets for breeders (Chapter 3). It seems then that it is beneficial to retain dominance in a good quality territory and long-term relationships could be a side effect of it.

Since my study found no substantive benefits of mate retention, I hypothesise that birds should be willing to abandon a breeding position and move to a better situation if they have the chance, and in Chapter 4, I explore why then breeders divorce. Divorce is a common strategy in pairs socially bonded to first-order relatives (incestuous). Reproductive success for these pairs is severely reduced (Kingma et al. 2013) and to find divorce as an escape of incest is an expected outcome. However, divorce is not only an incest-avoidance mechanism but also a strategy in pairs of unrelated individuals. Here, females appear to be the main beneficiaries of divorce and they most likely initiate the dissolution of the pair

bond, by taking breeding positions on territories of higher quality (Fig. 3, Chapter 4).

However, no improvement in immediate reproduction is found and this challenges what is known about the adaptive value of divorce. My findings offer a new understanding on the fitness benefits obtained and the complex interplay of factors in the decision to leave a partner.

In summary, studying aspects of productivity in purple-crowned fairy-wrens has shown that this species faces important constraints in partner choice that will eventually affect reproduction. My thesis has shown that successful reproduction is a hard-to-reach outcome due to external environmental pressures and that long-term pair bonds are not a key to improve productivity. Instead, large groups and territories of high quality have consistently show up as key benefits for productivity that also drive competition for breeding vacancies. All these characteristics could be common place in tropical species, especially for those that occupy territories year-round and live in saturated environments. Furthermore, in this thesis I have dealt with ecological patterns that are not common in other systems, such as year-round reproduction, multi-brooding, high rates of nest predation and long periods of fledgling survival. Such patterns may prevent using common existing methods in animal ecology, since they were developed to study species from different environments that have fixed seasonal reproductive cycles facing different selective pressures. Investigating more tropical species will help to develop further integrated methodologies that will allow to explore similar measures in other species. To date, we are only starting to understand which processes affect reproductive success and which ecological and/or social pressures are relevant for tropical birds.

My research also highlighted some potential threats of climate change. In here, an increase on climate extremes (both rainfall and temperature) might have implications in the slow reproductive benefits that purple-crowned fairy-wrens obtain at each breeding attempt (Fig. 1, Chapter 2). Hopefully my results highlighting the importance of good habitat quality for nest success, breeder dispersal, and support for large social groups, will not only inform, but provide support for the ongoing successful management for the habitat of this species (Skroblin et al. 2014). Although, we might better understand the threats of ongoing climatic change, due to a better understanding of the nature of these threats and as the duration of the study increases; however, their occurrence cannot be avoided nor their direct effects mitigated. Thus, due to their slow pace of reproduction of this species, and the threats of ongoing climatic change, preservation of significant stretches of healthy habitat supporting growing populations, is urgently needed.

In conclusion, my results exploring which ecological and social factors determine variation of individuals' productivity will contribute to a core aspect of life-history theory. Moreover, this information will be particularly relevant to understand the slow pace-of-life of tropical species; information that is key to manage threatened species.

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