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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:

<b>Nature of contribution</b>	<b>Extent of contribution (%)</b>
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:

<b>Name</b>	<b>Nature of contribution</b>
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  $\pm$  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 ( $\beta$ ) 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 =  $20 \pm 11$  weeks, after failed nests =  $5 \pm 8$  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  $2.93 \pm 0.05$  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,  $\Delta$  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  $\beta = 0.06 \pm 0.05$ ,  $p = 0.27$ ,  $\Delta$  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.

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

<b>(b) Arthropod abundance</b>	<b>Predictor</b>	<b>Effect</b>	<b>SE</b>	<b>Z</b>	<b>p</b>
	Rainfall (cm)	<b>0.16</b>	<b>0.01</b>	<b>2.09</b>	<b>&lt;0.001</b>
	Rainfall <sup>2</sup> (cm)	<b>-0.14</b>	<b>0.01</b>	<b>-2.83</b>	<b>&lt;0.001</b>
	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.

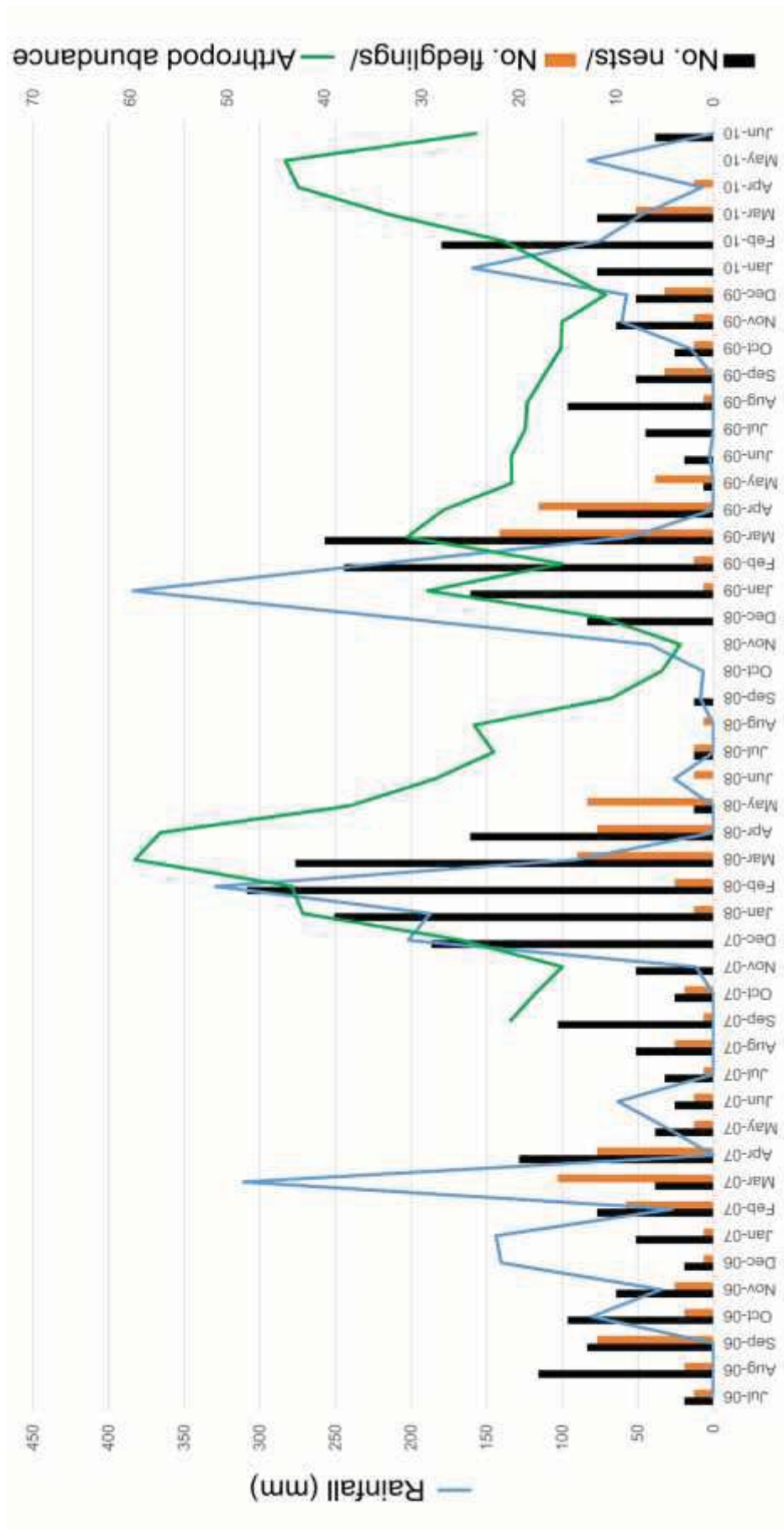
Response variable	(a) Clutch size (2-4)			(b) Number of fledglings (0-4)*			(c) Nestling condition (body mass, g)**		
	Estimate	SE	p	Estimate	SE	p	Estimate	SE	p
<b>Number of observations</b>	n = 532 nest (171 pairs)			n = 192 nests (111 pairs)			n = 357 nestlings (160 nests)		
<b>Fixed effects</b>	Estimate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

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

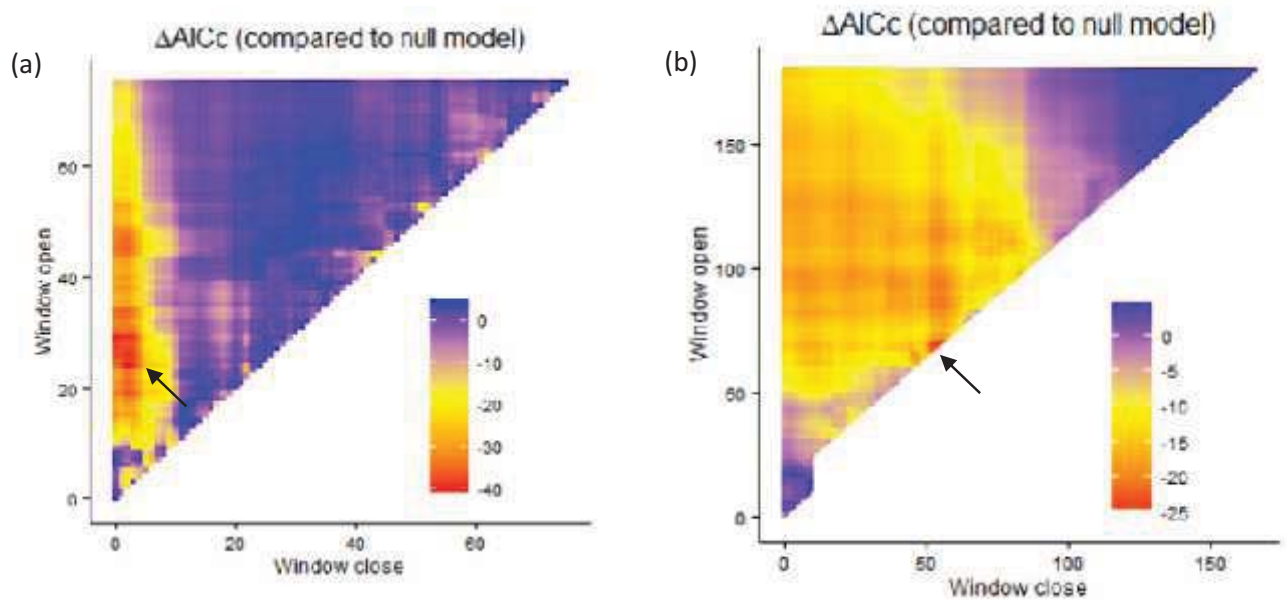
\*\*body mass on day 7.

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

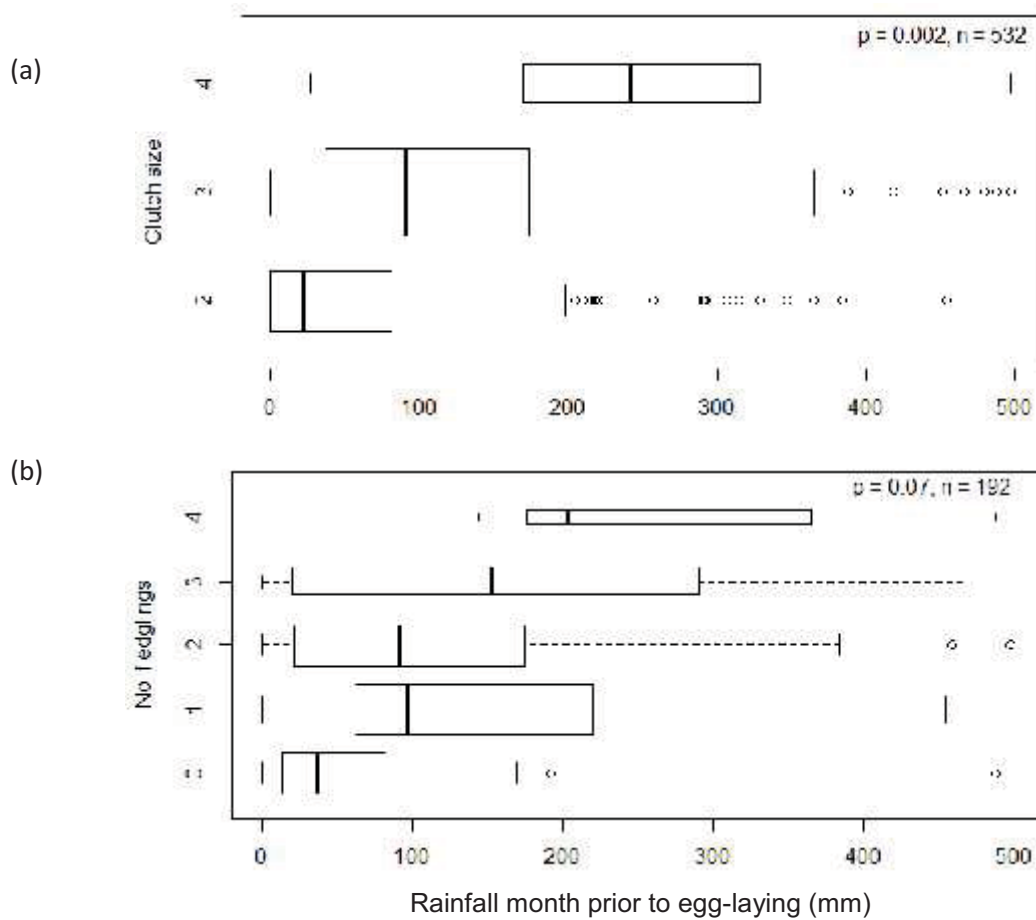
**Figure 1.** The number of territories initiating nests (black columns) is a response that follows cumulative rainfall of the previous month (blue line). Arthropod abundance follows rainfall with approximately 2 month-lag (green line). The number of fledglings surviving 6 weeks after fledging (orange 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 to 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.

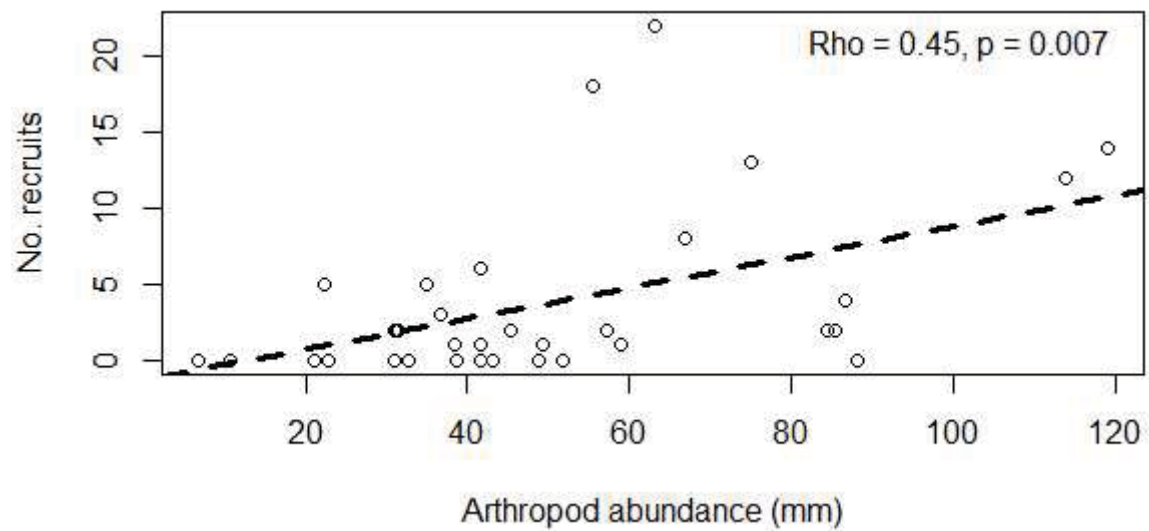
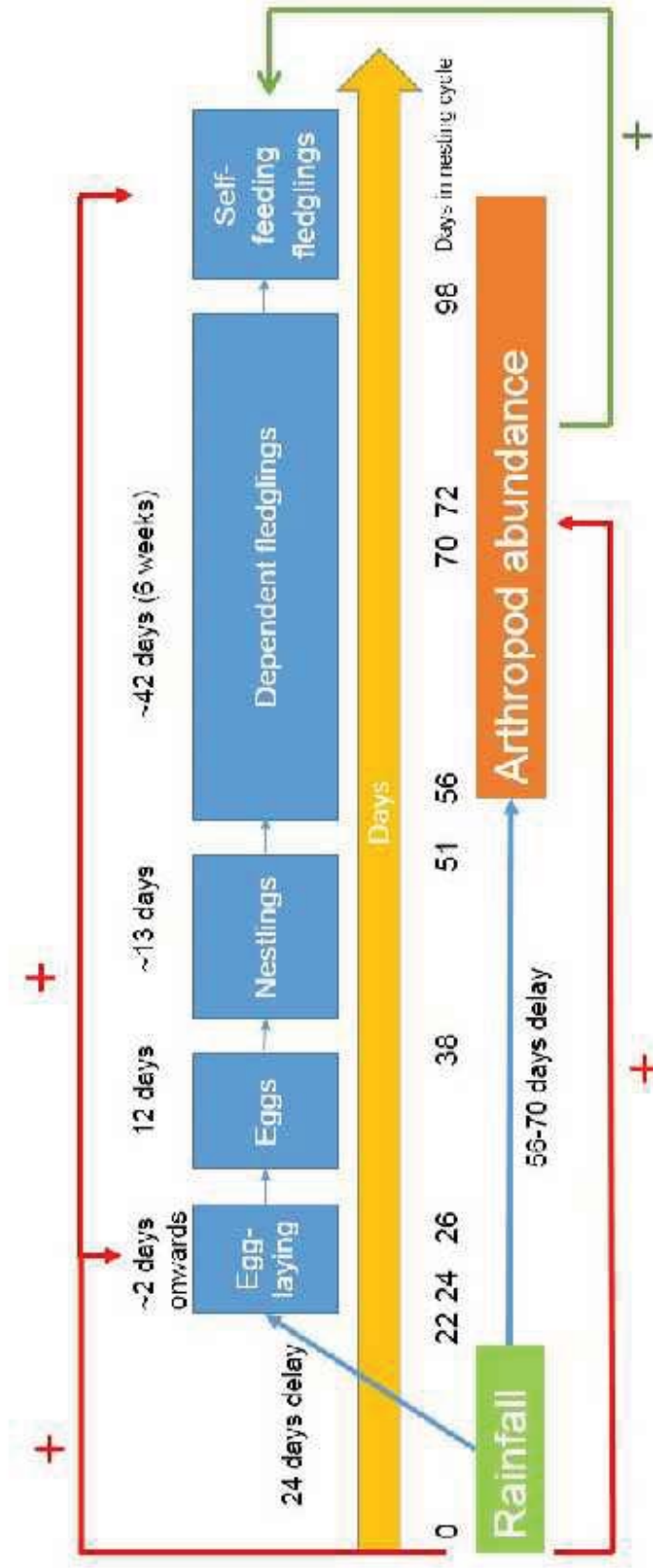


Figure 5. Schematic representation of timing of rainfall in relation to nesting initiation and arthropod abundance. Red arrows represent the positive effect of cumulative rainfall during the critical climate window on clutch size, number of fledglings surviving to 6 weeks (recruits) and arthropod abundance, 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  $\Delta\text{AICc}$  with most negative values first.  $\Delta\text{AICc}$  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)

<b>Nesting</b>	$\Delta\text{AICc}$	<b>Window opens</b>	<b>Window closes</b>	$\beta$	<b>SE</b>	$\omega$
	-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

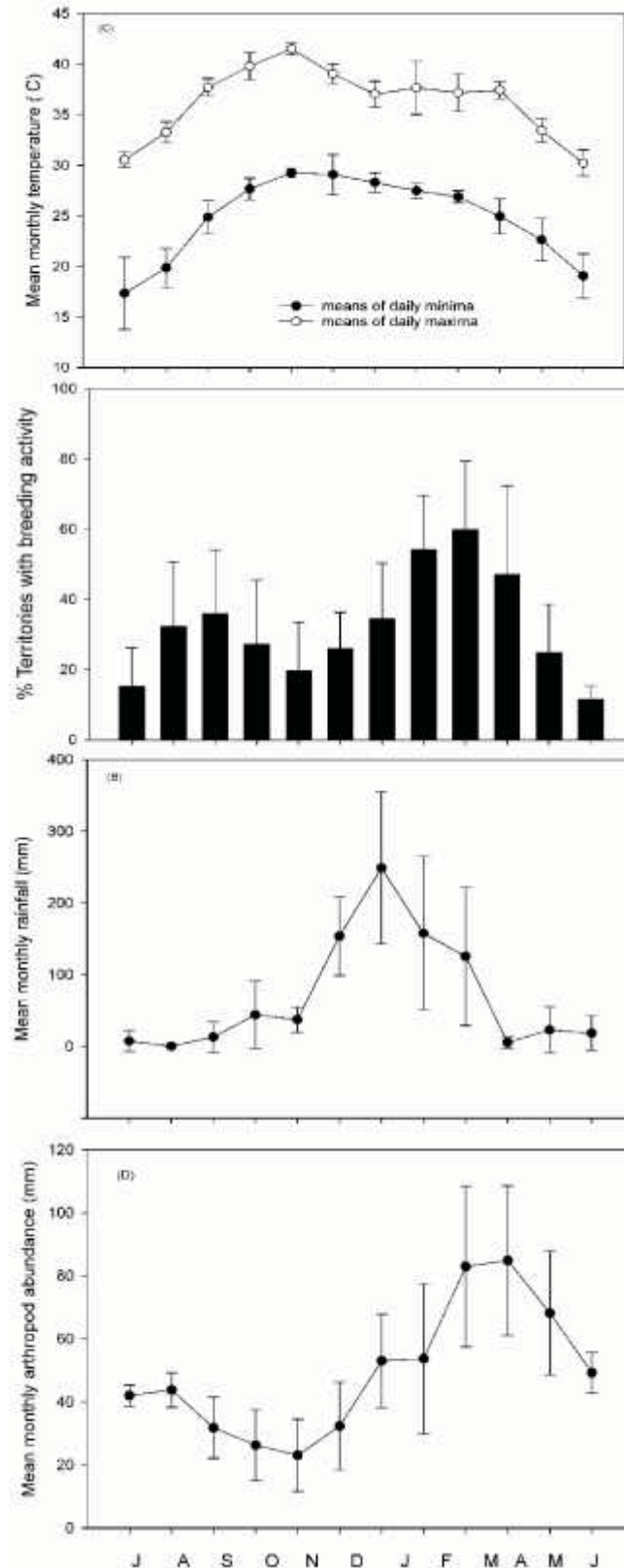
(b)

<b>Insect abundance</b>	$\Delta\text{AICc}$	<b>Window opens</b>	<b>Window closes</b>	$\beta$	<b>SE</b>	$\omega$
	-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 ( $\Delta AICc$ ) 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  $\Delta AICc$  (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  $\sim 300$  days). Strongly supported windows are grouped together. For further information refer to van de Pol et al. (2016).

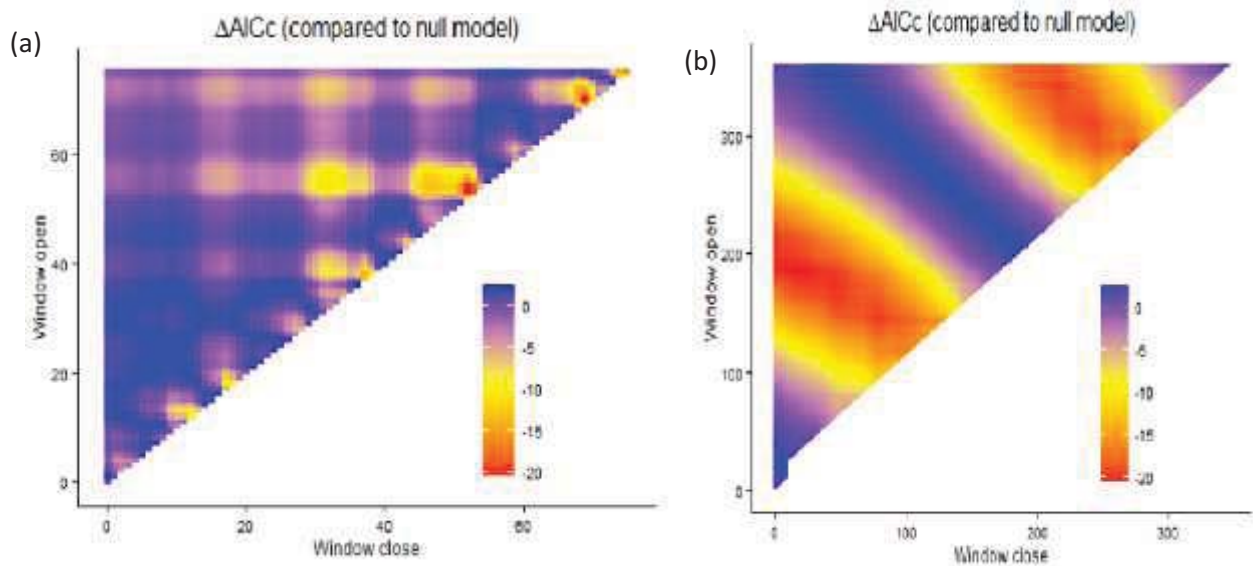


Figure S3. Proportion of focal watches when fledglings were fed (black line) or when they found their own food (dotted line). The number of fledglings observed in each age category is shown at the bottom of the graph.

