

**The impact of parental traits, offspring traits, and climate on parental care during the incubation stage
in a tropical bird**

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ABSTRACT

Many factors could play a role in individual variation in amount and length of parental care. We studied parental care during the incubation period of the Black-capped antshrikes (*Thamnophilus atrinucha*) in central Panama. Our comprehensive data set allowed us to determine the impacts of parental traits (age and sex), offspring traits (time of year and age of young), and climate (rain and temperature) on variation in parental care within the species. We found that an interaction between sex and age of the adult influenced incubation behavior, while time of the year and age of young did not alter incubation. Perhaps most important, was rain's significant impact on parental care, with more care in drier years. These results have conservation implications for future parental care, juvenile recruitment, and population trends of the antshrike in the face of a changing tropical climate.

KEYWORDS

Parental care, antshrike, nest, egg, adult age, sex, rainfall, temperature

INTRODUCTION

Parental care is facing new challenges with a changing climate. How rainfall in particular, and other traits of the adults and the environment impact parental care in the nest is rarely studied in tropical species. These changing climates could make parental care more stressful for species. Nevertheless, this information is critical given climate is predicted to become drier in Panama and changes in parental care strongly impact juvenile survival (Solomon et al., 2007; Tarwater & Brawn, 2010; Tarwater, Ricklefs, Maddox, & Brawn, 2011).

Parental care is any investment a parent puts into its offspring, from nest building to provisioning of offspring (Ghalambor & Martin, 2001; Gross & Sargent, 1985; Sargent, Taylor, & Gross,

1987). Increased parental care is predicted to increase the survival of offspring, with the amount and length of care strongly impacting probability of recruitment. Given that juvenile survival has been shown to have large effects on population growth, alterations in parental care can indirectly contribute to changes in populations (Cam, Monnat, & Hines, 2003; Clark & Martin, 2007; Remeš & Matysioková, 2016). Despite the benefits of increased care to offspring, this may come at a cost for parents in terms of future survival and reproduction (D. M. Bryant, 1979; Clutton-Brock, 1991; Ekman & Askenmo, 1986; Lack, 1966). Therefore, different strategies of parental care are used depending upon the environment and survival prospects of adults and offspring.

Given the potential costs of reproduction, adults may adjust their parental care depending upon traits of the parents, the offspring, and environmental conditions that alter survival of offspring and adults. For example, older adults and females are predicted to provide more parental care than younger adults and males. Parental care behavior is centered around an optimization problem: survival of young against survival of parent to breed again (Montgomerie & Weatherhead, 1988). This problem is used to predict the behavior of adults in parental care. Older adults have lower reproductive value (because they are closer to death) and thus may be willing to exert more effort into reproduction than younger adults (Montgomerie & Weatherhead, 1988). Furthermore, older adults may be capable of providing more parental care at less of a cost to themselves than younger adults because of increased experience in breeding and acquiring resources (Tarwater & Arcese, 2017). Traits of the offspring, including offspring age and date of birth/laying, are also found to influence parental care. For example, multiple studies have found that older young receive more care owing to their higher probability of survival, and thus increased reproductive value (Cézilly, Tourenq, & Johnson, 1994; Williams, 1966). Offspring birth/lay date can influence the probability of offspring survival and increased parental care is predicted for offspring that have a higher probability of survival. In most studies, offspring born or laid earlier in

the breeding season have higher survival and thus greater care is predicted for these offspring of higher value.

Environmental conditions, such as precipitation and temperature, can also impact parental care strategies and predictions vary depending upon temporal scale. Most studies on birds focus on temperature in temperate climates, and have found colder temperatures are associated with more care overall (Kendeigh, 1952). Rainfall has been ignored throughout avian parental care literature, but is an important factor to evaluate as more rain increases ectoparasites and also influences resource availability, specifically insects and fruit food availability in the tropics (Karr, 1976; Merino & Potti, 1996).

The scale of these environmental conditions is also very important and can be examined on a daily, monthly, or yearly scale. Different time scales can allow us to look at behavioral changes, adaptations, and evolution. Daily time scales focus more on the energy budget of the adult, immediate resource availability, and the immediate threat of keeping the chick alive (D. M. Bryant, 1975; David M. Bryant & Westerterp, 2002). The larger time scales determine the resource availability and prey behavior (Karr, 1976).

Our study examined how multiple traits influence parental care in a tropical bird species. We studied a tropical forest understory insectivore, *Thamnophilus atrinucha* (Black-capped antshrike, hereafter antshrike), in a Central Panama population that has been studied since the 1970s (J. D. Brawn, Karr, Nichols, & Robinson, 1999; Jeffrey D. Brawn, Benson, Stager, Sly, & Tarwater, 2017). The tropics are predicted to have the strongest impacts from climate change and tropical understory insectivores in particular are predicted to be particularly sensitive to changing environments (Şekercioğlu, Primack, & Wormworth, 2012; Tewksbury, Huey, & Deutsch, 2008). Recent work in Panama has shown that the majority of understory birds are negatively impacted by longer dry seasons and that recruitment of juveniles into the population is impacted more than adult survival (Brawn et al. 2017). Nevertheless,

what stage in the recruitment process (nest period, post-fledging period, independent period) is impacted by changes in rainfall is unknown. Furthermore, previous work on antshrikes has shown that date of laying and nestling mass, two traits impacted by parental care, impact juvenile survival (Tarwater et al., 2011). We examined parental care during the incubation period in 2015 (El Niño- dry wet season) and 2016 (La Niña- wet wet season). We asked the following research question: How do traits of the parents, traits of the offspring, and climate affect incubation patterns? We evaluated incubation using three different metrics- nest attentiveness, on-bouts, and off-bouts (for predictions see Table 1). Attentiveness is used as an indication of overall parental care, while on-bouts and off-bouts reflect different strategies of adults that must balance the needs of their offspring with their own needs and with variation in predators and food resources.

METHODS

Study population and site

Parental care in antshrikes was studied on a 100 ha plot (9°9'35"N, 79°44'36"W) located within Parque Nacional Soberanía, a 20,000 ha forest in central Panama, in 2015 and 2016 (Robinson, Brawn, & Robinson, 2000). Antshrikes are year-round territorial understory insectivores (Tarwater & Kelley, 2010). They are sexually dimorphic, exhibit biparental care, and are genetically monogamous with low divorce rates (Tarwater, Brawn, & Maddox, 2013; Tarwater & Kelley, 2010). The species has a model clutch size of two and can have multiple broods during their long breeding seasons (lasting 5-9 months depending upon the year) (Tarwater & Kelley, 2010). Parental care was studied between February – August each year, encompassing both the dry season and wet season. Birds were individually marked with color leg bands for identification. The incubation period for antshrikes is 16 days from the lay date of the first egg to hatching, and 14 days from the lay date of the second egg (Tarwater & Kelley, 2010). Nestling period length is 10 days from hatching to fledging (eggs that hatch later in the day will fledge one day later than normal; (Tarwater & Kelley, 2010). Antshrikes experience high nest predation with nest success per day

of 0.94 in older forests (80% nest predation; (Tarwater & Brawn, 2010)) and 0.91 in younger forests (96% nest predation; (Roper, 2005)).

Monitoring and videotaping

Focal territories on the plot were searched for nests ($n = 39$ nests). Nests were monitored every 2-3 days until offspring fledged or the nest failed. Lay date, hatch date, fledge date, clutch size, and survival were estimated from nest monitoring. Nests were videotaped in the incubation period ($n = 56$ days) for a minimum of 120 min/day (range= 147.18 – 666.1, avg.= 374.49 min/day). Cameras were set up throughout the incubation (range= 1 – 13, avg.= 7.92 days old) and between 7:00 am and 7:00 pm (average start time= 8:13). Effects of video camcorders on Antshrikes are minimal as previous studies have seen adults returning to nests within 15 minutes of placing the camcorders (Tarwater & Brawn, 2008, 2010).

Incubation Period

Parental care during the incubation period was assessed using three metrics - attentiveness, on-bouts, and off-bouts. Attentiveness was calculated as the sum of all the time spent incubating eggs, including any cleaning or rotating of eggs. On-bout is defined as average length of time a parent was on the nest and was estimated by summing all of the time spent incubating eggs divided by the number of incubation periods. Off-bout is defined as the average length of time a parent was off the nest and was estimated by summing all of the time spent off the nest divided by the number of off periods. These metrics reflect individual variation in care- on-bouts and off-bouts- to adapt to predation and resources, while also reflecting the overall care given to the offspring attentiveness. Attentiveness, on-bouts, and off-bouts were calculated on a per nest basis and for each sex separately.

Factors that influence parental care

We examined whether traits of parents, the offspring, and climate influenced parental care during the incubation and nestling periods. Two traits of parents were examined - sex and age. Sex was

recorded from the nest videos. Age was estimated using a novel method for calculating age from song (for details see (Tarwater & Kelley, 2018)). In brief, we took vocal recordings of parents (N= 50 individuals, 24 male, 26 female) using Marantz PMD660 MKII handheld 24-bit SD recorder. For each individual, 1-9 loud songs (median = 7, avg. = 6.48 ± 0.25) were isolated using Adobe Audition v3.0. Each song was analyzed for three song metrics (syllable rate, number of total syllables, and frequency dispersion) using the Program R. These metrics were then used to determine age of the individual (range = 1.39 – 12, avg. = 5 ± 0.3) (for details see Kelley and Tarwater, unpubl. data).

We examined two traits of the offspring - age of young and time of year. We did not include clutch size as a metric because clutch size was typically two in the IP (78.57% of nests). Age of young was estimated using data collected from nest monitoring. If the nest was found after lay date, hatch date or fledge date was used to estimate age of young. If the young did not survive to hatch, age of eggs was considered unknown. Time of year was examined using the Julian date of the day filmed (range = 83 – 238, avg. = 158.38 ± 2.14).

Climate was examined at different time scales (daily, monthly, and yearly) for both rain and temperature. Data for rain and air temperature was gathered from a nearby weather station, located 8 km away and managed by the Smithsonian Tropical Research Institute. Electronic data download of air temperature (average, 15 min frequency) and rain (total, 5 min frequency) was used to calculate average daily temperature (Celsius) and total daily rain (mm). Monthly and yearly average temperature and total rain were gathered from the monthly summaries data sheets. 2015 was a strong El Niño year (dry wet season- wet season total rain = 1601.6 mm) with a wet season ranked 47 out of the past 48 years, while 2016 was a strong La Niña year (wet wet season – wet season total rain = 2773.5 mm; from 1971 – 2016 wet season total rain – range = 1595.3 – 3506.0 mm, avg. = 2329.1 ± 66.7 mm) with a wet season ranked 8 out of the past 48 years (see Smithsonian Tropical Research Institute Physical Monitoring Program for details).

Statistical Analysis

We used program R 3.2.2 (R Development Core, 2008) to examine what influenced parental care. Nest attentiveness (total number of minutes), on-bouts (average number of minutes/on-bout), and off-bouts (average number of minutes/off-bout) were analyzed using linear mixed effects models (LME – Gaussian error distribution) with territory as random effect and an offset for the number of minutes a nest was recorded. Two models were run for each response variable, one overall model for the nest (e.g., total attentiveness for the nest) and another for each sex (e.g., attentiveness of the male parent for the nest). Overall models were run with a random effect of territory and fixed effects of age of young, daily rain, daily temperature, Julian date, monthly rain, and year. Per sex models were run with a random effect of nest ID and fixed effects of adult age, daily rain, Julian date, monthly rain, sex, year, adult age x sex, daily rain x sex, and sex x year. Both overall and per sex models were offset by the time recorded. Monthly temperature was not included because of a high correlation between monthly rain and monthly temperature (correlation = -0.9). For all other variables, weak correlations were observed, with variance inflation factors <3 (Zuur, Ieno, & Smith, 2007).

Model selection was done using the package MuMIn and Akaike's Information Criterion corrected for small sample sizes (AIC_c). We tested all nested models from the global model, except random effects were retained in all models (overall model N= 56 days; per sex model N= 112 days). If there was not one clear top model (top model contained <95% of the weight), we derived model averaged estimates to account for model uncertainty. This was done by averaging models with a cumulative Akaike weight of >0.95 from the top model and using maximum likelihood for parameter estimation (Anderson & Burnham, 2002). R² was calculated for all analyses following Nakagawa and Schielzeth (2013).

RESULTS

Climate had the largest effect on the incubation period with year having a significant impact on two of the parental care metrics and a weak effect on the third metric. Rain also had significant effects on the incubation period in both daily (weak effect) and monthly time scales. Only one parental trait (adult age) had an impact on the incubation period, and no offspring traits had an impact on the incubation period. Females were more responsive than males to rain in the incubation period.

Parental Traits

An interaction between adult age and adult sex was the only metric to impact incubation behavior and no other parental traits influenced attentiveness, on-bouts, or off-bouts (Table 3). Older females had shorter on-bouts than younger females, while males experienced no change in on-bouts based on age (Figure 2b).

Offspring Traits

Offspring traits, including age of young and Julian date, did not influence incubation behavior (Table 2, Table 3, and Table 4).

Climate

Year x sex had a significant effect on off-bouts (Table 4) and a weak effect on on-bouts (Table 3), but no effect on attentiveness (Table 2). Males and females had shorter off-bouts in 2016 (Figure 3a). Both sexes also had shorter on-bouts in 2016, but males had longer off-bouts than females in 2016 and shorter off-bouts than females in 2015 (Figure 2a). Year also had a significant effect on overall attentiveness (Table 2). Both males and females decreased their attentiveness in 2016 (Figure 1). Monthly rain x sex only had a significant effect on off-bouts per sex (Table 4). Females increased their off-bouts with more monthly rain, while male off-bouts did not change (Figure 3b). Daily rain had a weak effect on overall on-bouts (Table 3). Daily temperature and daily temperature x sex had no effect during the incubation period.

DISCUSSION

Our detailed data collection allowed us to see what factors (parental traits, offspring traits, and climate) influenced parental care in the incubation period in a tropical bird species. Our results show that rain, a factor usually not included in temperate studies, has a significant effect on parental care in the tropics. We also saw that sex and age of the adult were the only significant factors not related to climate, with females being more responsive than males during the incubation period.

Parental Traits

The result of older females having shorter on-bouts than younger females was opposite of our prediction that older adults would provide more parental care. Although these older females may provide more care at less of a cost to themselves, they still provide less care to the eggs (Tarwater and Arcese 2017). This may be due to the condition of the parents, which was not analyzed in this study. Females condition may worsen more than males at older age, causing them to require shorter on-bouts so that they can take care of self-maintenance (food, preening, etc.) more often. This female only age effect on parental care has not yet been found in other studies.

Offspring Traits

No offspring traits were significant during the incubation period. These traits are likely to be more significant in the nestling period, when young grow and require food, rather than just requiring parents to be on the nest, as shown with many previous studies (Williams 1966; Cézilly et al. 1994).

Climate

Temperature did not influence incubation behavior at any time scale in this tropical bird species. This factor has played a major role in temperate studies; however, studies have shown that it is likely not the only variable that explains parental variation (Conway & Martin, 2000).

Rain strongly impacted incubation in our study, with El Niño and La Niña years having a significant effect on attentiveness, on-bouts, and off-bouts. Overall, there was less parental care in the

wet wet season than the dry wet season. With few studies having looked at rains impact on parental care, we suggest more research is needed to be done on how rainfall impacts parental care, food resources, and predators. More data should also be collected on variation in timing and length of rain. Less parental care in the drier years could be due to its impact on insect behavior or parent self-maintenance. This result also shows that lower recruitment of juveniles into the population in longer dry seasons is not due to less parental care in the incubation period. Other periods of parental care, including nestling and post-fledgling, should be studied to determine if parental care is significant in explaining this decrease in juvenile recruitment.

With a changing climate predicted for Panama, our results show that parental care in tropical antshrikes will likely change. This change will be more related to changes in rain than temperature. This care and its imminent changes should continue to be studied in order to better understand future population and juvenile recruitment trends.

FIGURE CAPTIONS

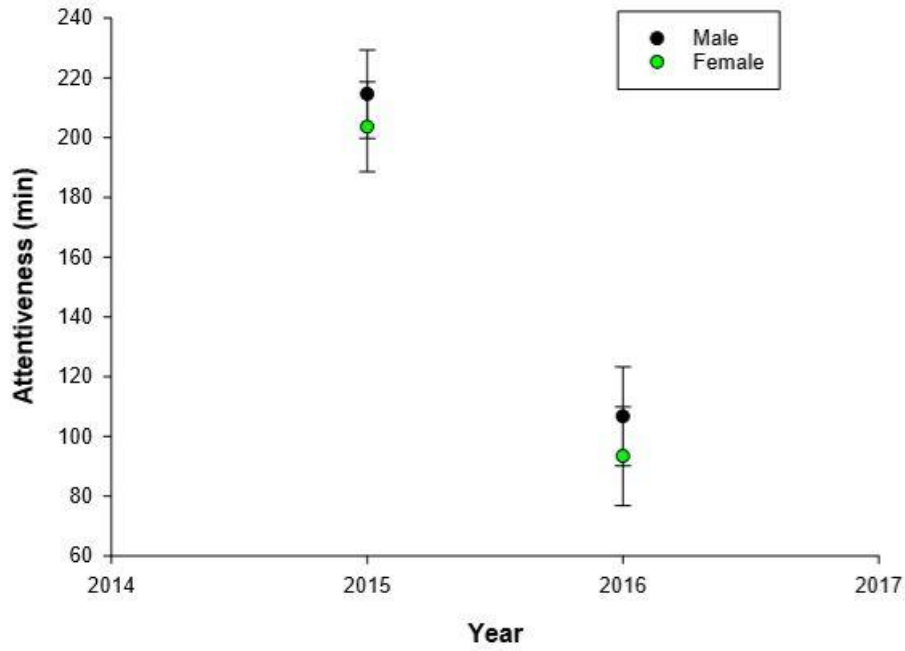
Figure 1. Variation in nest attentiveness per year in antshrikes for the entire nest (squares) and by males (closed circles) and females (open circles). Values are based on model output from the LME and SE bars are shown.

Figure 2. Variation in on-bouts per year (a) and with adult age (b) in antshrikes by males (closed circles, a, and black line, b) and females (open circles, a, and green line, b). Values are based on model output from the LME and SE bars (a) and 95% CI (b) are shown.

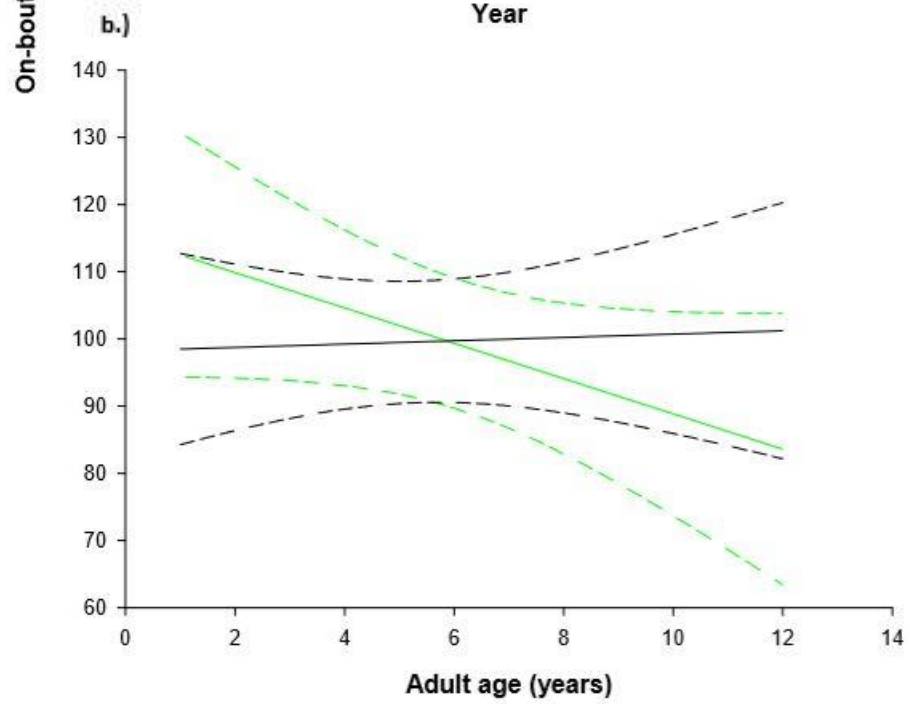
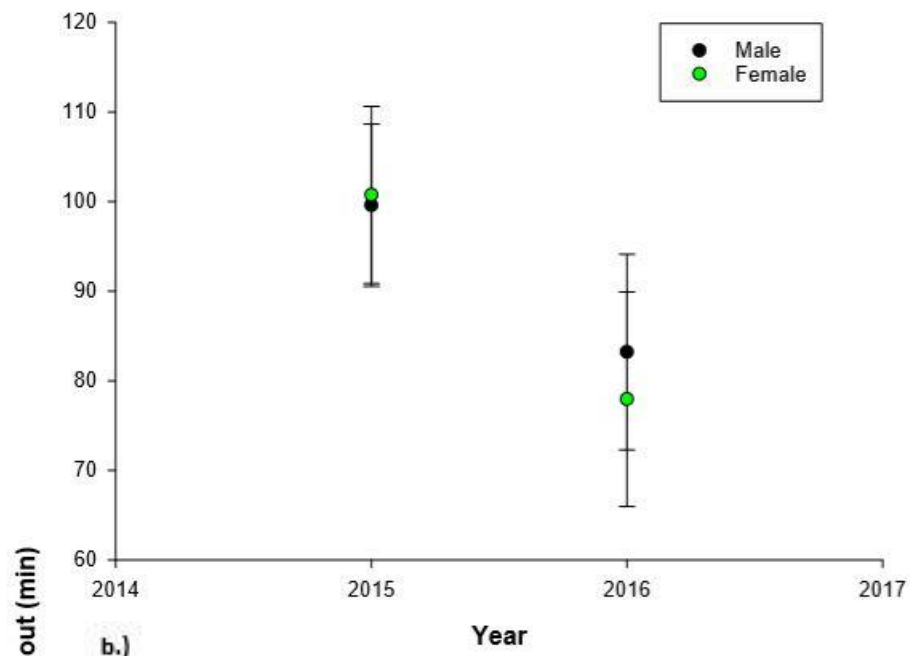
Figure 3. Variation in off-bouts per year (a) and with monthly rain (b) in antshrikes by males (closed circles, a, and black line, b) and females (open circles, a, and green line, b). Values are based on model output from the LME and SE bars (a) and 95% CI (b) are shown.

FIGURES

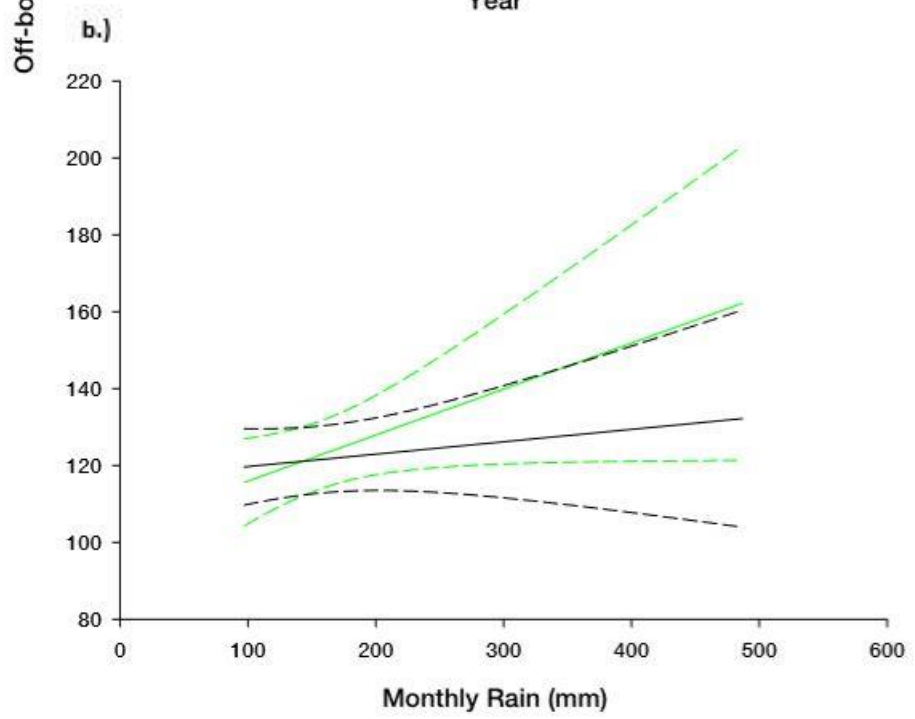
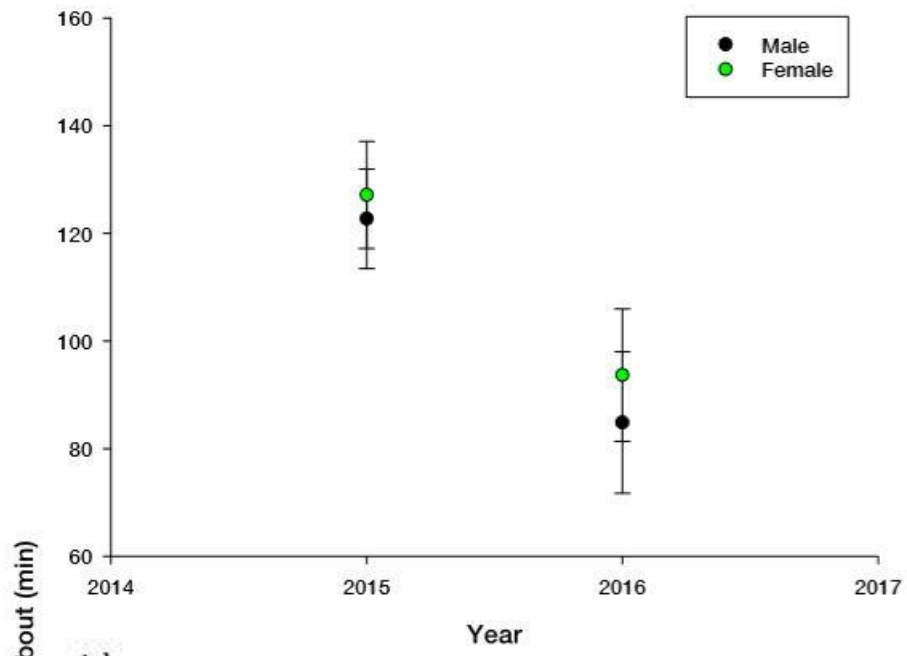
1.)



2.) a.)



3.) a.)



TABLES

Table 1. Depicts the predictions of each predictor variable along with the reasoning behind each prediction.

Predictor Variable	Prediction	Reasoning
Age of parent	Older parents provide more care	Higher reproductive value or lower costs of reproduction
Sex of parent	Males and females exert same levels of care	Biparental care with low extra-pair paternity (Tarwater et al., 2013)
Age of young	Older offspring receive more care	Higher reproductive value given higher survival probability (Tarwater & Brawn, 2010; Tarwater et al., 2011)
Time of year	Offspring hatched later in the breeding season receive more care	Offspring hatched later in the year have delayed dispersal and higher survival (Tarwater & Brawn, 2010)
Daily temperature	Care increases with colder temperatures	Colder temperatures lead to higher energetic costs of developing embryos (Booth, 1987)
Daily rain	Care increases with more daily rain	More daily rain leads to increased ectoparasites and increased brooding requirements (Antoniazzi et al., 2011; Radford, McCleery, Woodburn, & Morecroft, 2001)
Monthly rain	Care increases with more monthly rain	More annual rain leads to larger distribution and abundance of resources
Annual rain	Care increases with more annual rain	More annual rain leads to larger distribution and abundance of resources

Table 2. Model-averaged results of the influence of parental traits, offspring traits, and climate on nest attentiveness. Results are shown for the overall model and for the per sex model.

Traits	Overall β estimate	Overall SE	Overall Lower CI	Overall Upper CI	Per Sex β estimate	Per Sex SE	Per Sex Lower CI	Per Sex Upper CI
Attentiveness	420.00	206.05	-3.52	843.51	222.23*	45.39*	131.65*	312.82*
Year (2016)	-197.43*	40.33*	-281.77*	-113.09*	-5.29	11.89	-30.17	19.59
Daily rain	-1.98	2.17	-6.54	2.58	-1.07	0.63	-2.34	0.20
Monthly rain	0.18	0.23	-0.30	0.66	0.02	0.13	-0.25	0.29
Daily temperature	-6.32	15.43	-38.69	26.04	NA	NA	NA	NA
Julian date	0.12	0.86	-1.69	1.93	-0.20	0.46	-1.13	0.73
Age of young	0.85	6.98	-13.79	15.48				
Age of Adult	NA	NA	NA	NA	-3.45	3.94	-11.30	4.39
Daily rain x Sex	NA	NA	NA	NA	-0.74	-0.74	-0.74	-0.74
Sex (male) x year (2016)	NA	NA	NA	NA	1.05	1.05	1.05	1.05
Adult age x sex (male)	NA	NA	NA	NA	-2.84	-2.84	-2.84	-2.84
Monthly rain x sex (male)	NA	NA	NA	NA	1.36	1.36	1.36	1.36

Note:

CI, 95% confidence interval

*Confidence intervals (CI) do not cross 0. All terms whose CI do not cross 0 have a P value of <0.05 for the model average model.

Table 3. Model-averaged results of the influence of parental traits, offspring traits, and climate on nest on-bouts. Results are shown for the overall model and for the per sex model.

Traits	Overall Estimate	Overall SE	Overall Lower CI	Overall Upper CI	Per Sex Estimate	Per Sex SE	Per Sex Lower CI	Per Sex Upper CI
On-bout	66.30	80.92	-98.46	231.07	114.10*	32.42*	49.70*	178.49*
Daily temperature	3.60	4.65	-6.13	13.33	NA	NA	NA	NA
Monthly Rain	-0.04	0.06	-0.17	0.10	-0.06	0.09	-0.25	0.12
Daily Rain	0.42	0.64	-0.91	1.74	0.79	0.55	-0.31	1.88
Year (2016)	-5.29	11.89	-30.17	19.59	-29.29	14.53	-58.70	0.13
Julian Date	-0.04	0.26	-0.57	0.50	0.06	0.28	-0.50	0.62
Age of Young	-0.38	1.86	-4.28	3.52	NA	NA	NA	NA
Adult Age	NA	NA	NA	NA	-4.39	2.78	-9.92	1.15
Sex (male)	NA	NA	NA	NA	-27.04	33.93	-94.09	40.02
Adult Age x Sex (male)	NA	NA	NA	NA	7.78*	3.66*	0.44*	15.12*
Daily Rain x Sex (male)	NA	NA	NA	NA	-1.33	0.74	-2.80	0.15
Sex (male) x year (2016)	NA	NA	NA	NA	27.56	20.61	-13.72	68.84
Monthly Rain x Sex (male)	NA	NA	NA	NA	0.17	0.11	-0.04	0.38

Note:

CI, 95% confidence interval

*Confidence intervals (CI) do not cross 0. All terms whose CI do not cross 0 have a P value of <0.05 for the model average model.

Table 4. Model-averaged results of the influence of parental traits, offspring traits, and climate on nest off-bouts. Results are shown for the overall model and for the per sex model.

Traits	Overall Estimate	Overall SE	Overall Lower CI	Overall Upper CI	Per Sex Estimate	Per Sex SE	Per Sex Lower CI	Per Sex Upper CI
Off-bout	40.62	53.87	55.91	-68.97	84.47	44.45	44.96	-3.64
Age of Young	1.41	1.20	1.28	-1.10	NA	NA	NA	NA
Julian Date	-0.20	0.19	0.20	-0.59	0.36	0.29	0.30	-0.22
Year (2016)	5.56	8.60	9.17	-12.42	-34.88*	16.26*	16.79*	-67.79*
Daily Temperature	-2.11	3.05	3.25	-8.48	NA	NA	NA	NA
Monthly Rain	0.03	0.05	0.05	-0.07	0.18	0.11	0.11	-0.04
Daily Rain	0.05	0.39	0.41	-0.76	-0.11	0.51	0.52	-1.12
Adult Age	NA	NA	NA	NA	-1.78	2.08	2.13	-5.95
Sex (male)	NA	NA	NA	NA	18.07	29.08	29.39	-39.54
Adult Age x Sex (male)	NA	NA	NA	NA	-1.40	3.92	4.00	-9.24
Daily Rain x Sex (male)	NA	NA	NA	NA	0.94	0.82	0.83	-0.69
Sex (male) x year (2016)	NA	NA	NA	NA	-20.62	26.66	27.14	-73.80
Monthly Rain x Sex (male)	NA	NA	NA	NA	-0.23*	0.12*	0.12*	-0.46*

Note:

CI, 95% confidence interval

*Confidence intervals (CI) do not cross 0. All terms whose CI do not cross 0 have a P value of <0.05 for the model average model.

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