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EFFECT OF PARENTAL CARE AND NEST ATTENDANCE ON REPRODUCTIVE SUCCESS IN WOOD STORK (*MYCTERIA AMERICANA*)

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SUMMARY

I. Introduction

Parental care, i.e. any pre- and post-breeding investment made by a parent that increases offspring survival (Trivers 1972; Westneat and Sherman 1993; Royle *et al.* 2012), has evolved in multiple lineages independently to maximize individual fitness, benefiting the selfish genetic interests of parents (Gross and Sargent 1985). Parental care includes, among others, oviposition, site selection or construction, production of eggs containing important nutrient reserves (Sargent *et al.* 1987), feeding, lactation, transport, incubation, and protection against predators (Seki *et al.* 2007). As a crucial element in reproductive systems, parental care has received considerable empirical and theoretical attention in the past decade (Göth *et al.* 2004; Klug and Bonsall 2010), much of which focused on sex differences in parental care (Mcnamara *et al.* 2000; Kokko and Jennions 2008) and the amount of care provided (Westneat and Sherman 1993; Gross 2005).

Many possible strategies for parental care coexist in the animal world, from the absence of parental care, to cooperative breeding in which the brood is taken care by more than two individuals (Gross and Sargent 1985; Mcnamara *et al.* 2000; Cockburn 2006). However, in a large majority of species, female contribution to parental care significantly exceeds male contribution (Trivers 1972). Several hypotheses have been proposed to explain this pattern. Generally, it is widely accepted that different investment by the two sexes emerges as a consequence of differential cost-benefit trade-off between male and female (Smith 1995), which results in an antagonistic dynamic between sexes (Houston *et al.* 2005; Pingault and Goldberg 2008). In fact, when male and female carry out parental care together, their genetic interests can diverge creating sexual conflict (Chapman *et al.* 2003). Indeed, both parents are generally unrelated to each other, and either of them can benefit by abandoning the current brood and transferring the total cost of care to their partner (Trivers 1972; Houston *et al.* 2005). Thus, sexual conflict may affect the relative effort in parental care of male and female parents (Chapman *et al.* 2003). The genetic interests of males and females can diverge for a variety of reasons. For example, anisogamy, i.e. initial asymmetry in pre-mating parental investment via the production of gametes could favor an even more marked divergence in post-mating parental care (Trivers 1972, Kokko and Jennions 2008). Larger ova being typically costlier than spermatozoa, females would be more compelled than males to provide care because they risk to lose a greater initial investment (Trivers 1972). On the other hand, external fertilization could foster paternal care: in externally fertilized species, females usually lay earliest, and males then fertilize the eggs. To increase certainty of paternity, male territoriality is often associated to external fertilization, and could lead to a more prevalent paternal care (Gross and Shine 1981; Gross and Sargent 1985). Additionally, in species with external fertilization, early release of gametes by females could also cause female desertion leaving males to take care of eggs (Gross and Sargent 1985; Beck 1998).

As a consequence of this conflict, exclusively paternal or maternal care occurs more often in nature than biparental care (Wesolowski 1994). In birds, however, the overwhelming majority of species, dispenses biparental care (> 90 %; see; Silver *et al.* 1985; Cockburn 2006; Harrison *et al.* 2009). Several hypotheses have been proposed to explain the evolution of parental care in birds. For instance, the vast majority of birds are nidicolous (> 80 %; see Ar and Yom-Tov 1978). In contrast to nidifugous species (also called "precocial" species), the progeny of nidicolous species (also called "altricial" species) is totally dependent from their parents, which calls for a higher amount of post-zygotic parental care (Silver *et al.* 1985), and mostly results in biparental care in nidicolous species as opposed to mainly uniparental care in nidifugous species. However, some authors have argued that the progeny's demand for care does not affect parental cooperation strategies in birds (Remeš *et al.* 2015). Parental cooperation defined as the extent of biparental care, varies along a continuum from approximately equal share by the male and female (AlRashidi *et al.* 2011) to obligate uniparental care, whereby one parent (the male or the female) provides all care to the offspring (Remeš *et al.* 2015).

Male-biased operational sex ratio (OSR), i.e. higher male than female abundance in the population, should lead males to adopt strategy of caring for offspring rather than deserting them and then face stiff competition in acquiring a new partner (Ar and Yom-Tov 1978; Liker *et al.* 2015). Harsh and variable climatic conditions (Klug and Bonsall 2010; Jetz and Rubenstein 2011; Remeš *et al.* 2015) or an increased nest predation level (Wesolowski 1994) could create a need for steady monitoring of eggs and offspring, so that uniparental care could not be sufficient, favoring biparental care. Other ecological and biological factors have been proposed such as: mating system (Emlen and Oring 1977), sexual specialization for some care (Kokko and Jennions 2008; Barta *et al.* 2014) or relative mass of laying (in percentage of female weight) (Silver *et al.* 1985). Altogether, these factors fail to explain care evolution towards biparental care in some cases (Royle *et al.* 2016). For instance, some species of plovers exhibit all forms of parental care apart from cooperative care (Reynolds and Székely 1997). Hence, parental care is highly complex, both in terms of characteristics and behaviors expressed and in terms of factors underlying the evolution of these traits. Parental care evolution appears to be the result of a dynamic and multivariate process that entail the coevolution of multiple traits in males, females and descendants (Royle *et al.* 2016).

Wood Storks (*Mycteria americana*) are one of the largest species of wading birds (Rodgers *et al.* 1995). The southeastern U.S breeding population of Wood Storks (in the states of Alabama, Georgia, South Carolina, and Florida) has declined sharply during the past century. The number of breeding pairs in the United States decreased from about 20,000 pairs in the 1930s to 10,000 pairs in the early 1960s (US Fish and Wildlife Service 2007) and between 2,500 and 5,000 pairs in the late 1970s (Ogden *et al.* 1987). Subsequently, the species was listed as endangered under the Endangered Species Act in 1984 (Bancroft *et al.* 1992; Coulter *et al.* 1999). Recent recover of the population led to a downlisting of Wood Stork to threatened in 2014 (FWS 2015), but accurate estimates of breeding success are still needed to monitor the status of the species population and its recovery (Bryan and Robinette 2008).

Wood Stork belong to *Ciconiidae* family composed of 17 species of storks distributed throughout the world (FWS 1999, 2007) and is the only stork species breeding in the United States (FWS 2007). Adults ranges from 80 to 110 cm of height, weigh about 2-3 kg and can reach a wingspan of 170 cm (Kahl 1964; Rodgers *et al.* 1995; Coulter *et al.* 1999). Plumage is white, except for black iridescent primary and secondary feathers and black tail (Coulter *et al.* 1999; FWS 1999, 2001). Its geographical range extends from the southeastern United States to the north of Argentina (Ramo and Busto 1992), through eastern Peru, Brazil, Venezuela, northwestern Ecuador, Central America, Mexico and Cuba (FWS 1999). Wood Stork feed mainly of fish (Kahl 1962, 1972; Ogden *et al.* 1976), in 15–50 cm deep water bodies (Kahl 1964) using a nonvisual myo-tactile foraging technique known as "tactolocation" (Kahl 1964; Clark 1979, 1980; Griffin *et al.* 2008).

Wood Storks are gregarious and philopatric birds (Kahl 1964; Frederick and Ogden 1997). They seem to form new pair bonds every nesting season, but apparently stay monogamous during a single nesting season (Kahl 1972). Wood Storks customarily establish colonies in high enough trees in swamps or on islands surrounded by relatively large bodies of water (FWS 1999). Some colonies are known to have been active for more than 60 years (Coulter *et al.* 1999), whereas others are active only for one or two years (Frederick and Meyer 2008). Their nesting cycle is about 4 months long (Kahl 1964; Kushlan 1986; Coulter *et al.* 1999); it used to historically start between October and December in the southern Everglades until 1962 (Kushlan 1986), but then the onset of nesting gradually shifted to between December and March (Kahl 1964).

Wood Storks lay asynchronously (Kahl 1972; Werschkul 1979) between 1 and 5 eggs (Kahl 1964; Coulter and Bryan 1995), with an average of 3 eggs a lay (Rodgers 1990; Rodgers and Schwikert 1997). Incubation lasts 28 days and is equally split between male and female (FWS 2001). During incubation, at least one parent remains constantly at the nest. The mean fledging success is generally 2.5 per nest and per breeding season (Coulter and Bryan 1995; Rodgers and Schwikert 1997; Bryan and Robinette 2008). Nestlings remain in the nest for 50 to 60 days before taking their first flight (Kahl 1972; Coulter *et al.* 1999). The responsibility for nest guarding appears to be evenly distributed between the two parents (Griffin *et al.* 2008) and both parents feed their progeny by regurgitation on the nest floor (Kahl 1962, 1972) and participate busily in nest construction (FWS 2001). After the first week, chicks start to be brooded only at night and during cold periods (Clark 1980) and this behavior fades out after the second week. After the third week, the time spent by parents at the nest decreases considerably (Bryan *et al.* 1995, 2005), primarily due to bigger size of nestlings and the appearance of aggressive behavior of nestlings to any approach (conspecifics, other bird species, humans) (Kahl 1972) allowing them to be sufficiently independent to defend themselves. After leaving the nest for the first time, young chicks continue to return at the nest for parental foraging and night rest for another 1 to 3 weeks (Kahl 1972; Borkhataria *et al.* 2012).

Many factors are known to affect Wood Stork reproductive success, such as predation (Rodgers 1987), human disturbances (Bouton *et al.* 2005), which may also indirectly increase predation (González 1999), toxic chemicals (Fleming *et al.* 1984; Burger *et al.* 1993), storms associated with strong winds (Coulter and Bryan 1995; Bryan and Robinette 2008), as well as physiological factors such as age or hormone levels (Burger 1982). However, reproductive success seems to be mostly related to prey availability in the environment (Griffin *et al.* 2008), which is in turn related to air temperatures (Kahl 1964; Coulter and Bryan 1995) and precipitation (Clark 1979; Frederick and Collopy 1989; Gaines *et al.* 2000). Finally, intraspecific aggression can have a significant impact on reproductive success (Coulter and Bryan 1995). Indeed, more than a third of nests from a colony may experience take-overs in some years, primarily during incubation (Bryan and Coulter 1991).

In this study, our aim was to examine the relationship between the number and duration of foraging flights and reproductive success in Wood Storks and how nest takeovers can interfere with it. Throughout this study, we were interested in answering two research questions. First, we wanted to determine if there is a variation in parental foraging behavior during offspring development and whether such variation affects reproductive success. The growing demand of offspring to be fed during their development led us to formulate the following predictions: P1: The number of foraging flights will increase with the advancement of offspring development while the mean duration of these flights will decrease; P2: A higher number of foraging flights results in a higher reproductive success. Second, we wanted to examine if the time spent at the nest explains the occurrence of observed takeover phenomenons and what role does it play in reproductive success of Wood Stork. The constant need for presence of at least one parent during egg incubation and the initial stage of offspring development led us to predict that: P3: the percentage of time spent at the nest simultaneously by both parents may reduce the occurrence of takeovers.

II. Material and Methods

Two Wood Stork colonies in urban areas were selected for subsequent data collection, namely Wakodahatchee Wetlands and BallenIsles. Throughout this report, it is important to emphasize that a colony is not a point in space (which is properly a colony site), nor a breeding aggregation from a specific animals' population (which is a local breeding population). Rather, a colony is a given reproductive animals' population at a given site for a specific period of time (Buckley and Buckley 1980).

1. Studies sites

a) Wakodahatchee Wetlands

Wakodahatchee Wetlands is a public park based on a constructed wetland that treats a portion of the Southern Region Water Reclamation Facility's (SRWRF) secondary wastewater effluent (Hobbs *et al.* 2003). These wetlands were designed to treat the secondary effluent with natural biological processes to further reduce nutrient levels (Crittenden *et al.* 2014). Wakodahatchee Wetlands is in the suburbs of Delray Beach (See Appendix 2), Florida, on the east side of Jog Road, between Woolbright Road and Atlantic Avenue (26°47'N, -80°14'W). The park was opened to the public in November 1996, and was officially designated operational in January 1997 (Bays *et al.* 2000). Wakodahatchee Wetlands was constructed on a 56-acre site with 39 acres comprising the wetland surface area (Bays *et al.* 2000; Hobbs *et al.* 2003; Crittenden *et al.* 2014). A 1.2-km long boardwalk crossing the wetland and a series of interpretive panels have been designed to inform and educate the public on natural systems and wildlife of the wetland (Bays *et al.* 2000; Hobbs *et al.* 2003; Crittenden *et al.* 2014). Marshes comprise about

70% of the wetland area, vegetated by native emergent, forested, and transitional wetland species designed to emulate native south Florida wetland plant communities. Non-exhaustively, we can cite: bulrush (*Scirpus validus, S. californicus*), duck-potato (*Sagittaria lancifolia*), sawgrass (*Cladium jamaicense*), Fakhahatchee grass (*Tripsacum dactyloides*), cypress (*Taxodiuhm ascendens*), pond apple (*Annona glabra*), dahoon holly (*Ilex cassine*) as well as sabal palm (*Sabal palmetto*) (Bays *et al.* 2000). Wakodahatchee Wetlands hosts one wading bird colony including pairs of Great Blue Heron (*Ardea herodias*), Anhinga (*Anhinga anhinga*) or Great Cormorant (*Phalacrocorax carbo*) in addition to Wood Stork. Within the colony, observations have been made on two different islands close to each other (about 55-m apart). Both islands are constituted by pond apple trees, and are almost entirely submerged by water, small terrestrial part being formed by tree roots. It was not possible to monitor all nests present on the two islands due to visibility and logistical limitations. Hence, we monitored a total of 32 nests, 17 on Island 1, and 15 on Island 2.

b) BallenIsles

The second colony is located in BallenIsles Country Club, a private resort created in 1963. Precisely, BallenIsles Country Club is located in Palm Beach Gardens, at the crossroad of Northlake Boulevard and North Military Trail (26°83'N, -80°11'W), 46.6-km North of Wakodahatchee Wetlands (See Appendix 2). The wading bird colony monitored in BallenIsles is situated on a single island with a large terrestrial part, unlike Wakodahatchee Wetlands. This island, and the water that surrounds it, are placed within a golf course where hundreds of practitioners come to perform each day. Again, due to visibility and logistic limitations, as well as the practice of golf activity, 29 nests were monitored in the island, 13 on the West side, and 16 on the South side. Wood Storks nested both in pond apple and Brazilian peppertree (*Schinus terebinthifolia*) on the West side and in Brazilian peppertree only on the South side. In addition, similarly to Wakodahatchee Wetlands colony, others wading birds nested in the same island, including Anhinga, Great Cormorant, Tricolored Heron (*Egretta tricolor*) or Great Egret (*Ardea alba*).

2. Data collection protocol

Observations were made over a period of 123 days, from January 31 to June 2 2017 throughout the nesting season to avoid time biases (Rodgers and Schwikert 1997). Two 5h-long surveys were performed each week on each site, once in the morning (7h30–12h30) and once in the afternoon (12h30–17h30). Monitoring was spread across the week as to homogenize time gaps between successive surveys at a single site (every 3.5 days). Moreover, using two observation posts at each site, we alternated the location of each observer weekly in order to avoid observer bias. Wood Storks' behavior was observed using 12 × 50 binoculars (Fujioka and Yamagishi 1981; Rodgers and Schwikert 1997) and recorded using an 18 to 55-mm Nikon D5300 lens digital camera and a 600-mm telephoto lens equipped with an electronic image stabilizer (Frederick and Meyer 2008; Griffin *et al.* 2008).

Data collection began either during the phase of nest building or at the beginning of the incubation period. We identified each individual Wood Stork based on unique skin pattern on their head (Clark 1980; Bryan and Coulter 1991). We took each side profile picture of every individual within breeding pairs, and built a photographic database of individual identities that was used for subsequent identification (See Appendix 2). Because Wood Storks lack evident sexual dimorphism, sexing partners of a pair was only possible when we witnessed copulation (Clark 1980; Fujioka and Yamagishi 1981; Bryan and Coulter 1991). The status of each nest (construction, incubation or post-hatching) was described at the beginning of each daily survey. We recorded weather conditions at the beginning of the monitoring and their changes throughout the duration of the survey. Parents' departures and arrivals in their nest were constantly monitored and recorded (Clark 1980; Bryan *et al.* 1995, 2005). Thanks to the individual identity database, data represent behavioral data for each individual monitored, rather than combined data for a pair as found in Bryan *et al.* (2005). We also noted parental behavior on return of nest (feeding, watering, nest construction or unknown) as in Bryan *et al.* (2005).

In order to avoid disturbance, we did not access Wood Stork nests to verify the presence of eggs and count them. However, laying dates were estimated from hatching dates, by subtracting an average incubation period of 28 days (Rodgers and Schwikert 1997) and were matched to observation of adults sitting in the nest for brooding. We were not able to examine hatching success, which can be defined as the average number or proportion of eggs that hatched in a nest (Ranglack *et al.* 1991). Instead, we counted hatchlings in each nest where visual counting was feasible. In addition, we were able to confirm our visual counts for a fraction of the nests in BallenIsles, thanks to a collaboration with PhD Candidate Betsy Evans (Florida Atlantic University), who accessed the island once per week in the early pre-flight stage and provided at-nest counts of chicks. Thus, we could evaluate reproductive success for each of these nest (N = 18). As in many other studies (Coulter and Bryan 1995; Gaines *et al.* 2000; Bouton *et al.* 2005; Vergara and Aguirre 2006; Rodgers *et al.* 2008), similarly to hatching success, reproductive success was estimated at each nest, as the proportion of hatched chicks still alive at time of fledging.

3. Statistical analysis

a) Changes in frequency and duration of foraging trips

We used growth curve analyses (Mirman 2014) to model both frequency and duration of foraging trips as a non-linear function of time (weeks since hatching) using generalized linear mixed models. The overall shape of the curve was captured with inclusion of orthogonal polynomials on time up to the fourth order, with individual-within-nest random effects of on all terms (for frequency only; for the duration analysis, the use of complete trips with known time of departure and arrival limited the sample size, and the estimation of random effects was not achievable). Using a subset of individuals of known sex, sex differences were tested with the inclusion of an additive and multiplicative fixed effect of sex. Similarly, the inclusion of an additive and multiplicative fixed effect of the start time of nesting allowed to test its effect on frequency and duration of foraging trips.

b) Effect of frequency of foraging trips on reproductive success ratio

For a number of nests, the number and fate of all hatchlings was collected, allowing the estimation of reproductive success ratio between 0 and 1 as the number of fledglings divided by the initial number of hatchlings. The effect of frequency of foraging trips on reproductive success ratio was then assessed using a logistic regression on the number of success (fledglings) and failures (hatchlings that did not survive until fledging). Fixed effect of the frequency of foraging trips during the early pre-flight stage (weeks 1–4) and during the late pre-flight stage (weeks 5–8) were included in the regression, after checking for their correlation.

c) Nest attendance and risk of takeover

Semi-parametric proportional hazards (SPPH) models were fit on the follow-up time of each nest before potential takeover, expressed as the week of the year (annual scale) or the week since start of incubation (biological scale). The instantaneous risk of takeover of a nest at a given week was modeled as a function of the baseline hazard experienced by all individuals, and the proportion of time with at least one adult or two adults present at the nest during the week. In the semi-parametric approach, weak assumptions about the baseline hazard are made, which allows the estimation of the relative risk of takeover. Covariate effects are then estimated using a partial likelihood that does not require estimating the baseline hazard.

All statistical analyses were performed in the software R 3.3.0 (R Core Team 2017) using notably the packages “lm4” (version 1.1.13; Bates *et al.* 2015), “survival” (version 2.40.1; Therneau and Grambsch 2000), and “cowplot” for graphs (version 0.7.0; Wilke 2016).

III. Results

Between January 31 and June 02, we monitored 61 nests on both sites (29 in BallenIsles, 32 in Wakodahatchee Wetlands), corresponding to 85 nesting attempts from identified Wood Stork pairs. From these, 27 underwent a takeover, 5 were abandoned, and 38 were monitored until fledging (See Appendix 3). For 29 nests in which the fate of the chicks from hatching till fledging was known, there was an average of 3.00 (±SD = 0.46) chicks that hatched per nest, and an average of 2.59 (±SD = 0.57) chicks that fledged per nest (Table 1).

Table 1: Number of nests broken down by the number of chicks per nest at the time of hatching (rows) and at the time of fledging (columns).

	1	2	3	Total
2	1	2	0	3
3	0	5	18	23
4	0	3	0	3
Total	1	10	18	29

1. Changes in frequency and duration of foraging trips

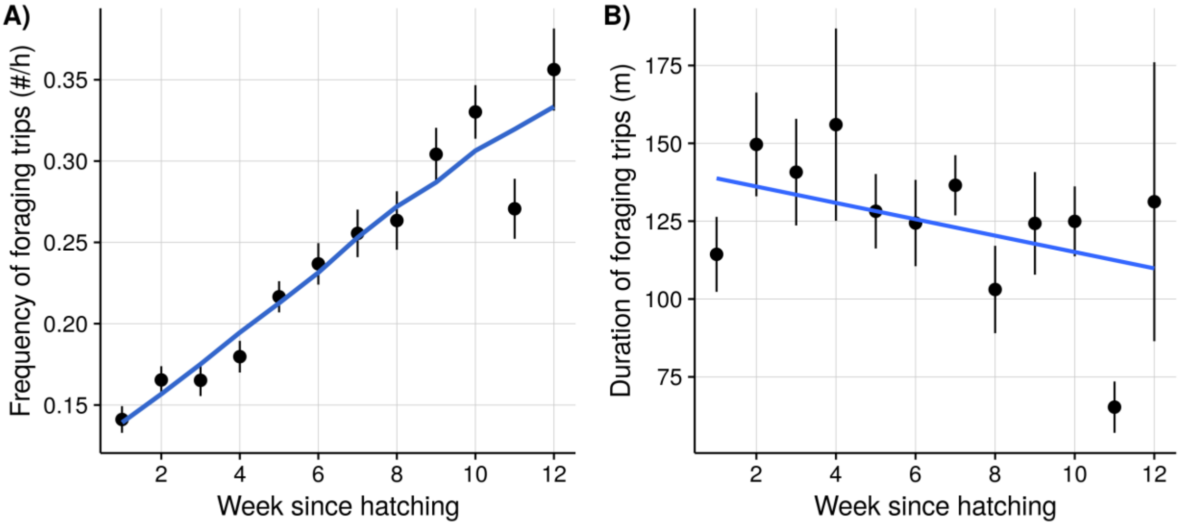

Figure 1: Frequency (A) and duration (B) of foraging trips through time during the post-hatching phase. Point represent average values for each week since hatching ± SE, and the blue line represents the best model fit (see text for details).

Adding orthogonal polynomials successively to the constant model of frequency of foraging trip significantly improved the fit until the quadratic term ($\chi^2(7) = 14.792$, $p = 0.039$; Table 2A), while adding a cubic or quartic term did not improve the fit further (resp. $\chi^2(1) = 1.011$, $p = 0.315$; $\chi^2(6) = 0.607$, $p = 0.436$; Table 2A). Using the cubic model as a baseline, model selection then showed that additive or multiplicative effect of sex did not significantly improve the fit (resp. $\chi^2(1) = 0.858$, $p = 0.354$; $\chi^2(2) = 1.463$, $p = 0.481$; Table 2B). Similarly, additive or multiplicative effect of the start time of nesting (did not improve the fit further (resp. $\chi^2(1) = 0.576$, $p = 0.448$; $\chi^2(3) = 5.503$, $p = 0.064$; Table 2C). The model including only the effect of first-, second- and third-order polynomials only was thus kept for rest of analysis. This model showed a highly significant effect of the first-order orthogonal polynomial term (0.225±0.06, $t(13.501) = 13.501$, $P < 0.001$; Table 3) demonstrating a positive linear relationship between the frequency of foraging trips and the week in chick development (Fig.1A).

Table 2: Model selection for frequency of foraging trip analysis in Wood Storks. *K* is the number of parameters in the model; AIC the Akaike Information Criterion, LL the log-likelihood, and χ^2, Df and Pr(>χ^2) indicates the statistic, the associated degrees of freedom and *p*-value for the comparison between each model and the previous one. The selected model is indicated in bold.

A) General shape

Model	*K*	AIC	LL	χ^2	Df	Pr(>χ^2)
Constant	4	-1197.7	602.83			
First-order polynomial	9	-1447.3	732.67	259.679	5	<0.001
Second-order polynomials	**16**	**-1448.1**	**740.07**	**14.792**	**7**	**0.039**
Third-order polynomials	17	-1447.1	740.57	1.011	1	0.315
Fourth-order polynomials	18	-1445.8	740.87	0.607	1	0.436

B) Sex effect

Model	*K*	AIC	LL	χ^2	Df	Pr(>χ^2)
Baseline	**16**	**-611.00**	**321.50**			
Sex (additive)	17	-609.86	321.93	0.858	1	0.354
Sex (multiplicative)	19	-607.32	322.66	1.463	2	0.481

C) Effect of the start date of nesting

Model	*K*	AIC	LL	χ^2	Df	Pr(>χ^2)
Baseline	**16**	**-1448.1**	**740.07**			
Start (additive)	17	-1446.7	740.35	0.576	1	0.448
Start (multiplicative)	19	-1448.2	743.10	5.503	2	0.064

Table 3: Coefficients and their significance of the best model for the frequency of foraging trips during the post-hatching phase.

Variable	Estimate	Std Error	Df	*t*	Pr(>|*t*|)
Intercept	0.225	0.006	47.1200	38.064	<0.001
First-order polynomial	**1.887**	**0.1403**	**42.630**	**13.501**	**<0.001**
Second-order polynomial	0.034	0.128	67.220	0.265	0.792

Conversely, adding orthogonal polynomials successively to the constant model of duration of foraging trip did not significantly improve the fit (all $p > 0.05$; Table 4A), although the first-order polynomial was very close to statistical significance ($F(1;155) = 3.612$, $p = 0.059$; Table 4A). We thus simplified the baseline model as a simple linear model including a main effect of the number of weeks since hatching. Using the simple linear model as a baseline, model selection then showed that additive or multiplicative effect of sex did not significantly improve the fit (resp. $F(1;68) = 0.427$, $p = 0.516$; $F(1;67) = 0.887$, $p = 0.350$; Table 4B). Similarly, additive or multiplicative effect of the start time of nesting did not improve the fit further (resp. $F(1;154) = 0.872$, $p = 0.352$; $F(1;153) = 2.559$, $p = 0.112$; Table 4C). The simple linear model including no effect of sex or start time of nesting was thus kept for the rest of analysis, and indicated a week trend of decreasing duration of foraging trips through time, although this effect was not significant at the 0.05 level (Table 5; Fig.1B).

Table 4: Model selection for duration of foraging trip analysis in Wood Storks. SSR and SSE are the residual, and explained respectively, sums of squares, with their associated degrees of freedom, and *F*, and Pr(>*F*) indicates the statistic and *p*-value for the comparison between each model and the previous one. The selected model is indicated in bold.

A) General shape

Model	SS_R	Df	SS_E	Df	*F*	Pr(>*F*)
Constant	**502825**	**156**				
First-order polynomial	491459	155	11366.4	1	3.612	0.059
Second-order polynomials	487172	154	4286.4	1	1.362	0.245
Third-order polynomials	481410	153	5762.2	1	1.831	0.178
Fourth-order polynomials	478286	152	3124.5	1	0.993	0.320

B) Sex effect

Model	SS_R	Df	SS_E	Df	F	Pr(>F)
Baseline	**236086**	**69**				
Sex (additive)	234611	68	1475.0	1	0.427	0.516
Sex (multiplicative)	231545	67	3066.5	1	0.887	0.350

C) Effect of the start date of nesting

Model	SS_R	Df	SS_E	Df	F	Pr(>F)
Baseline	**491459**	**155**				
Start (additive)	488720	154	2738.7	1	0.872	0.352
Start (multiplicative)	480680	153	8040.3	1	2.559	0.112

Table 5: Coefficients and their significance of the best model for the duration of foraging trips during the post-hatching phase.

Variable	Estimate	Std Error	t	Pr(>|t|)
Intercept	141.384	9.442	14.974	<0.001
Weeks	**-2.629**	**1.388**	**-1.893**	**0.060**

2. Effect of frequency of foraging trips on reproductive success ratio

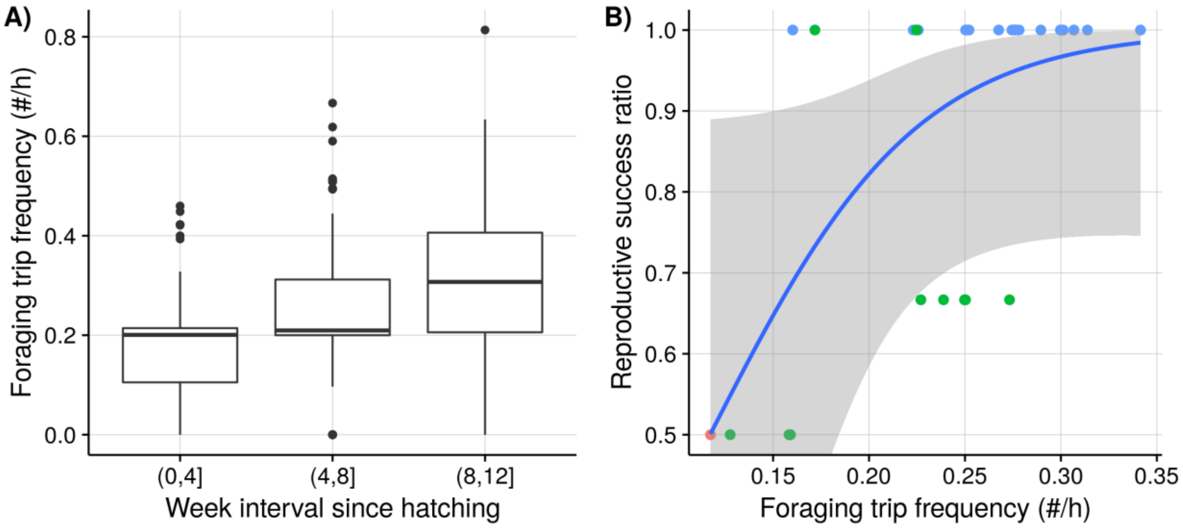

Figure 2: A) Frequency of foraging trips during the three stages of the post-hatching phase. B) Reproductive success ratio as a function of frequency of foraging trips. The color of dots indicates the number of fledglings in each nest (blue = 3; green = 2; red = 1) and the blue line indicates the logistic fit (with 95 % confidence interval).

The frequency of foraging trips increased during the three stages of chick development. The three stages were divided as follows: early pre-flight stage (weeks 1-4), late pre-flight stage (weeks 5-8) and post-flight stage (weeks 9-12) (Clark 1980). However, the effect of the frequency of foraging trips during the early pre-flight stage (weeks 1–4) on reproductive success ratio was not significant (Z=1.025; p=0.306; Table 6). On the other hand, the frequency of foraging trips during the late pre-flight stage had a significant positive effect on reproductive success ratio (Z=2.929; p=0.003; Table 6; Fig.2B). Note that the two variables of the foraging trip mean frequency during the early pre-flight stage and during the late pre-flight stage were not correlated with each other (r = 0.216, t(27) = 1.148, p = 0.261).

Table 6: Coefficients and their significance of the logistic model for reproductive success ratio.

Variable	Estimate	Std. Error	*Z*	Pr(>|z|)
Intercept	-3.481	1.593	-2.185	0.029
Early stage	8.527	8.320	1.025	0.306
Late stage	17.828	6.086	2.929	0.003

3. Nest attendance and risk of takeover

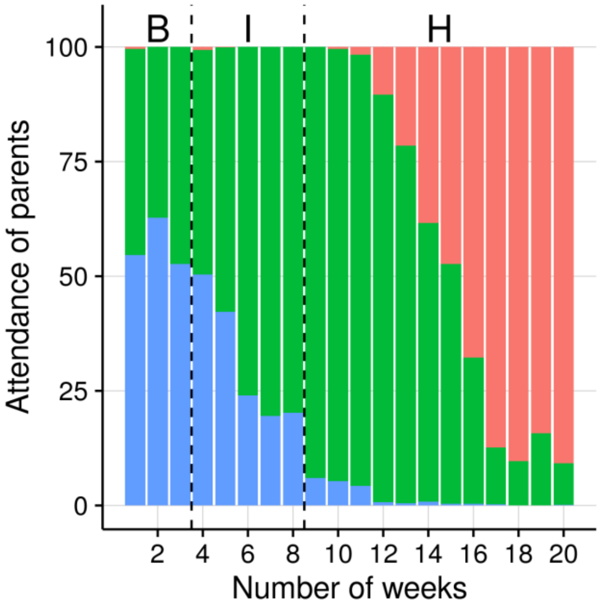

Figure 3: Nest attendance of adult Wood Stork through time. The color indicates nest attendance of 2 adults (blue), 1 adult (green) or none (red). B: building phase; I: incubation phase; H: post-hatching phase.

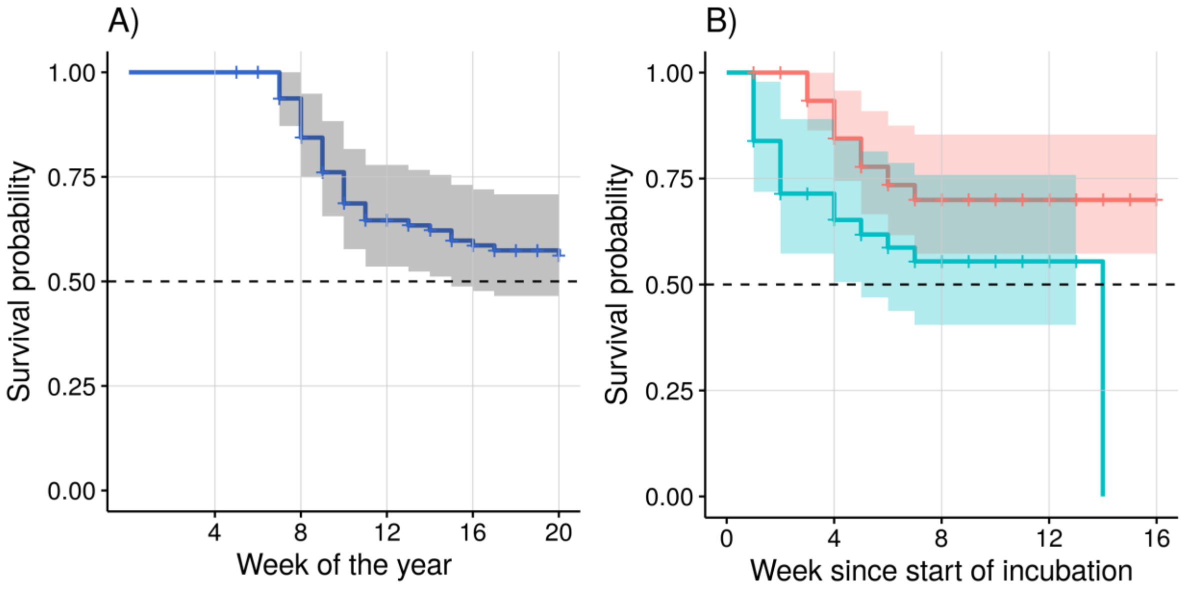

Figure 4: Kaplan-Meier survival curve (with confidence interval) for the risk of nest takeovers in 79 Wood Stork nests as a function of (A) the week of the year, or (B) week since start of incubation. Colors further distinguish between early pairs (red), and late pairs (blue).

Both adults were present more than half of the time at the onset of nesting; however, this proportion rapidly decreased during incubation. At the beginning of the early pre-flight stage, there was still a single adult constantly at the nest, before presence of adults altogether gradually decreased to around 10 % at the end of the nesting season (Fig.3). Most of the takeovers happened between weeks 7 and 11, i.e. from February 13 to March 19 2017 (Fig.4A). Finally, the survival model applied to the date of the beginning of the incubation shows that nest attendance of at least one parent did not significantly affect risk of takeovers ($Z = 1.289$; $p = 0.197$; Table 7) whereas the presence of both parents in the nest had a significant positive effect on the risk of takeover ($e^{\beta} = 1.017$; $Z = 2.506$; $p = 0.012$; Table 7). Similarly, the date of late initiation of incubation had a large positive effect on the risk of takeovers ($e^{\beta} = 2.135$; $Z = 1.971$; $p = 0.048$; Table 7; Fig.4B).

Table 7: Coefficients and their significance of the semi-parametric proportional hazards (SPPH) model applied to the risk of takeovers in Wood Stork nests. Exponentiated coefficients can be interpreted as multiplicative effects on the hazard, i.e. the instantaneous risk of takeover, holding other covariates constant. For instance, late starters have a risk more than twice higher than early starters ($e^{\beta} = 2.135$).

Variable	β	e^{β}	Std. Error	z	Pr(>|z|)
Presence ≥1 ad.	0.029	1.030	0.023	1.289	0.197
Presence 2 ad.	0.017	1.018	0.007	2.506	0.012
Late-starters	0.759	2.135	0.385	1.971	0.049

IV. Discussion

The complete monitoring of Wood Stork breeding season in two colonies in south Florida allowed us to address several hypotheses about reproductive success of this species as well as the occurrence of takeovers and their potential causes. The main results of this study showed that the frequency of foraging trips showed a gradual increase through time according to the developmental stage of the chicks, but was not influenced by sex or onset date of incubation. Conversely, the duration of foraging trips was also not affected by either sex, nor onset date of incubation, but only showed a slight decrease through time (P1 partially supported). In addition, reproductive success was influenced only by parental behavior in the late pre-flight stage when pairs with the greatest number of chicks were those with the higher frequency of foraging trips (P2 supported). Finally, we showed that most takeovers happened late February or early March, which made the first weeks of nesting also critical for nest success. Nest attendance of both individuals from a pair did not reduce the occurrence of takeovers, but late breeding pairs had a higher takeover probability than early pairs (P3 rejected).

Takeover behavior appears to be widespread in Wood Storks, where it may affect more than a third of pairs in a colony in some years (Bryan and Coulter 1991). In our study, 27 pairs underwent a takeover out of 85 pairs monitored (32 %). The occurrence of takeovers seems to correspond to certain weeks of the year, with the highest risk of undergoing intra-specific aggression observed between February 13 and March 19 2017. In addition, late pairs, initiating their nesting later in the year had more than twice the risk of undergoing a takeover than early pairs, which began nesting before the 6th week of the year. The majority of takeovers occurred earlier in the nesting period for late pairs, between the 1st and the 7th weeks, compared with only the 3rd and the 7th for the early pairs. The lower occurrence of takeovers in early pairs, could be explained by better intrinsic characteristics of individuals (Johnson and Kermott 1990) such as larger size, higher energy reserves, higher aggressiveness, or higher social status (i.e. dominance hierarchy rank). Although the existence of a dominance hierarchy is not documented in Wood Stork, it has been demonstrated in several bird species, where dominant birds are also more successful in acquiring and maintaining a territory (Hogstad 1999; Ratcliffe 2007). Our results also indicated that the time of simultaneous nest attendance by both individuals from a pair did not reduce the occurrence of takeovers. On the contrary, pairs with higher nest attendance of both individuals had a higher chance of undergoing a takeover. Even for the most diligent pairs, there are always needs that force them to leave the nest, leaving the one individual incubating unattended for at least a third of the time (see Fig.3). Moreover, Bryan and Coulter

(1991) showed that all takeovers occurred when a single individual was present in the nest, reinforcing the idea that susceptibility to takeovers mainly depends on intrinsic conditions of individuals. Although in our study a few takeovers happened during the post-hatching period, the majority occurred during the first few weeks of incubation (81.5%). Thus, this appears to be the most critical period of the breeding season for risk of takeover, after which the risk of intra-specific aggression declines and parents face different constraints in raising their offspring.

During the post-hatching phase, our results showed that the mean frequency of foraging trips per hour and their duration were not different between sexes. This results is partly in agreement with the literature. Indeed, Clark (1980) showed that the rate of male and female involvement in the foraging of young varied according to the pair. The male of a pair may be responsible for more than 60% of foraging trips, while in other pairs the number of foraging trips of males does not exceed 5% of that of females. Similarly, the mean frequency of foraging trips per hour and their duration were not influenced by the onset date of nesting. The presence of high temperatures as well as the scarcity of rains during the first 4 months of the year (data from National Oceanic and Atmospheric Administration (NOAA) located in Palm beach Int'I Airport and Boca Raton Airport) could be an explanation. In fact, hydrologic conditions of the wetlands surrounding the colony interact with landscape structure in determining how far and how often Wood Stork need to go forage to meet the energetic needs of their chicks (Coulter and Bryan 1993; Bryan *et al.* 1995).Dry weather conditions may have contributed to maintain a suitable level of water depth (15 to 25-cm, see Kahl 1962) for Wood Stork foraging (Clark 1979; Clark 1980; Griffin *et al.* 2008), in wetland habitats surrounding the colony, therefore not impacting the foraging behavior of individuals. On the other hand, the mean frequency of foraging trips per hour showed a gradual increase in time according to developmental stage of the chicks, consistent with the 3 accepted stages of development, i.e. early pre-flight stage (weeks 1-4), late pre-flight stage (weeks 5-8) and post-flight stage (weeks 9-12). However, after the 8th week, we have a lot of variation (some pairs decreasing, some still increasing) entailing too much noise to be very conclusive. The duration of foraging trips was not influenced by developmental stage of the chicks, with no significant change over time, although there may be a trend toward a decrease in the nesting season (Fig.1B). These results agree with the literature on Wood Storks. Indeed, all authors argue that the number of foraging trips increases with the advancement of young development (Clark 1980; Bryan *et al.* 1995, 2005) although duration of foraging trips stays constant throughout the development cycle (Bryan *et al.* 2005). As chicks develop, their energetic needs increase and the demand for food becomes higher (Khal 1962), while their need for protection decreases as they become able to thermoregulate and to defend themselves from aggressions (Clark 1980). Parents meet the increased energetic needs of chicks by increasing the number rather than the length of trips (Bryan *et al.* 1995). This idea is reinforced by the fact that the time of nest attendance by at least one adult drops steadily after the 4th week of development (Clark 1980; Bouton *et al.* 2005; see Fig.3), as the parents increase the frequency of foraging trips to feed their chicks, which in turn become more autonomous (Kahl 1972). Thus, in the late pre-flight stage, the frequency with which parents bring food to the chicks appears to be critical for their survival, and therefore, the parents' reproductive success. Despite the existence of a direct link between patterns of foraging trips and reproductive success in Wood Stork, this relation has never been quantified, to our knowledge.

Different distinct definitions of breeding success are available in the literature on birds. Some define breeding success as a simple on/off phenomenon (i.e. a nest is successful if it fledges at least one chick, and unsuccessful otherwise) (Robinson *et al.* 2000; Vergara and Aguirre 2006), some others as the number of fledglings produced per breeding season (Burger 1982), while some authors take into account the proportion of fledglings over the number of hatchlings, i.e. the initial brood size (De Steven 1980, Rotenberry and Wiens 1989). Hereafter, we define this proportion as reproductive success ratio. The opportunity of using one or the other definition is determined by the aim of each study. We used reproductive success ratio to assess the effect of the frequency of foraging trips during early and late pre-flight stages on Wood Stork reproductive success. Taking into account the number of chicks at the moment of fledging in relation to the number of hatchlings allows to provide a more accurate measure of how parental care in the early and late pre-flight stages affect nesting outcome. We showed that the mean frequency of foraging trips per hour in the early pre-flight stage did not affect reproductive success ratio, as opposed to frequency to the late stage. The highest reproductive success ratio (100%) corresponded to pairs exhibiting the highest mean frequency of foraging trips per hour (0.25 to 0.30 h^{-1}), while pairs obtaining the lowest reproductive success ratio (50%) had the lowest mean frequency of foraging trips per hour (0.12 to 0.15 h^{-1}) in our dataset. It is important to note the possible circularity in the approach: One could indeed argue that pairs that reached the late pre-flight stage with an already reduced brood size consequently decreased the frequency of trips due to reduced demands from the offspring. However, our results showed that the relationship between reproductive success ratio and frequency of foraging trips is independent of the absolute number of chicks. For instance, pairs that reached the late pre-flight stage with two chicks alive in the nest exhibited very contrasted foraging trip frequency (e.g.

about 0.15 to 0.25 h^{-1}, see Fig.2B, points in green) according to whether their initial brood size was also 2 (success ratio = 1) or they started with a larger brood size (success ratio = 3/2 or 4/2), while we would expect the same frequency if the number of fledglings would drive reproductive success. This result effectively supports an effect of foraging trip frequency in determining reproductive success ratio, and not vice-versa.

Our study showed that a delay in nesting initiation date could double the risk of undergoing takeover, but did not influence the frequency and duration of foraging trips. The link between late initiation date and higher risk of takeover suggests that takeover attempts may be less frequent at the very beginning of the breeding season than later. A possible explanation, again related to dominance hierarchy mechanisms, is that lower-rank individuals may recur to the strategy of taking over another pair's nest after trying unsuccessfully to establish their own. However, if the first nesting attempt fails due to takeover, Wood Storks are sometimes able to start a new clutch if the event occurred fairly early in breeding season (Bancroft *et al.* 1992). On the other hand, the nesting initiation date could also affect juvenile survival. In fact, rain events become more frequent later in the breeding season, altering water level conditions at foraging sites and potentially making it impossible for Wood Storks juveniles to forage properly with their " tactolocation " technique (Frederick and Collopy 1989; Ramo and Busto 1992). Thus, it appears that early initiation of nesting entails benefits on many levels. At the population level, the onset of the breeding season shifted from the historical records in the past decades as a consequence of hydrology alterations in South Florida (Kushlan *et al.* 1975), restricting the temporal window between the drydown that creates suitable foraging conditions for Wood Stork and the start of the rainy season. Today, it is recognized that nesting initiation is starting to return to historical values (Peter Frederick, personal communication). It is unclear whether this advancement, and presumably the consequent expansion of the temporal window for suitable nesting, will benefit more late-starters than early-starters.

Our study did not highlight a direct link between the number of fledglings and the mean frequency of foraging trips per hour in the early and late pre-flight stages. Other factors, therefore, seem to influence the number of fledging. For instance, predation from raccoons, the main predator of chicks in Wood Stork (Rodgers 1987), may affect young survival. Also, the asynchrony of egg hatching within a brood (Werschkul 1979), which results in a considerable difference in size between siblings, may cause starvation of younger ones (Kahl 1972). Furthermore, despite a strong human presence within these two colonies, disturbing behavior of Wood Storks by humans can be overlooked, Bouton *et al.* (2005) proving Woods Stork colonies can acclimate to humans. This statement could be checked in the field where some

Wood Stork pairs nested about 5 meters from the boardwalk in Wakodahatchee Wetlands.

Adult Wood Stork regularly travels substantial distances between colony and foraging sites (Kushlan 1986). The average distance traveled is usually within ~ 50 km, but for instance, Ogden *et al.* (1987) recorded Wood Storks foraging more than 130-km from their breeding colony. However, although the cost of foraging for chicks appears to be high in Wood Stork, our study showed that frequency of foraging trips did not differ between sexes. Ephemeral presence of shallow wetlands required for Wood Storks tactolocation behavior (Kahl 1964) could create an unpredictable availability of food resources (Bryan *et al.* 2012) which, coupled with the ever-increasing demand for food for chicks during their development (Kahl 1962) would force biparental care during the breeding season, a single parent not being enough to ensure reproductive success.

V. Conclusion

Many possible strategies for parental care coexist in the animal world (Cockburn 2006) and several hypotheses have been proposed to explain his evolution. For example, the hypothesis of anisogamy (Kokko and Jennions 2008), the mode of fertilization associated with male territoriality (Gross and Shine 1981; Gross and Sargent 1985) and the certainty of paternity (Møller and Birkhead 1993) have all been proposed as possible evolutionary mechanisms modulating the differential involvement of the two sexes in parental care. In birds, biparental care is the most common form (Harrison *et al.* 2009), and it seems that the mode of development of chicks, altricial or precocial (Silver *et al.* 1985), and male-biased operational sex ratio (Ar and Yom-Tov 1978; Liker *et al.* 2015) play an important role in making this an advantageous strategy in evolutionary terms. In Wood Stork, care for the young is performed by both parents (Clark 1980). During the incubation and the early pre-flight stage, brooding and protection of the chicks are critical and constrain at least one of the parents to attend the nest continuously (Clark 1980). In the later phases of development of the chicks, foraging behavior in order to provide food for the chicks becomes the most important part of care (Bryan *et al.* 1995, 2005). Our study revealed that the frequency of foraging trips increased as chick development progress and explained in part the reproductive success of this species. To our knowledge, this is the first study to explicitly relate patterns of foraging trips and nesting success from a quantitative standpoint in Wood Stork. Other variables may interact in determining nesting success, such as takeovers, where one-third of the monitored pairs were impacted by such intra-specific aggressions. However, our findings showed that increased attendance at the nest during the riskiest phases for intra-specific aggression did not reduce the occurrence of takeover.

To better understand factors shaping the behavior of Wood Stork during the nesting season, further investigations are still needed. Potential future research directions include the evaluation of the impact of environmental factors: Meteorological variables such as temperature, barometric pressure, humidity or wind speed would be interesting to study because they were shown to affect the number and duration of foraging trip in other bird species (Cartar and Montgomerie 1987). Moreover, it would be interesting to study the reproductive benefit of takeover behavior during the breeding season, comparing the benefit of this strategy with that of early-starters that build their own nest. Such investigation could provide insight about whether the reduced cost of not building a nest can increase success of individuals that adopt a takeover strategy.

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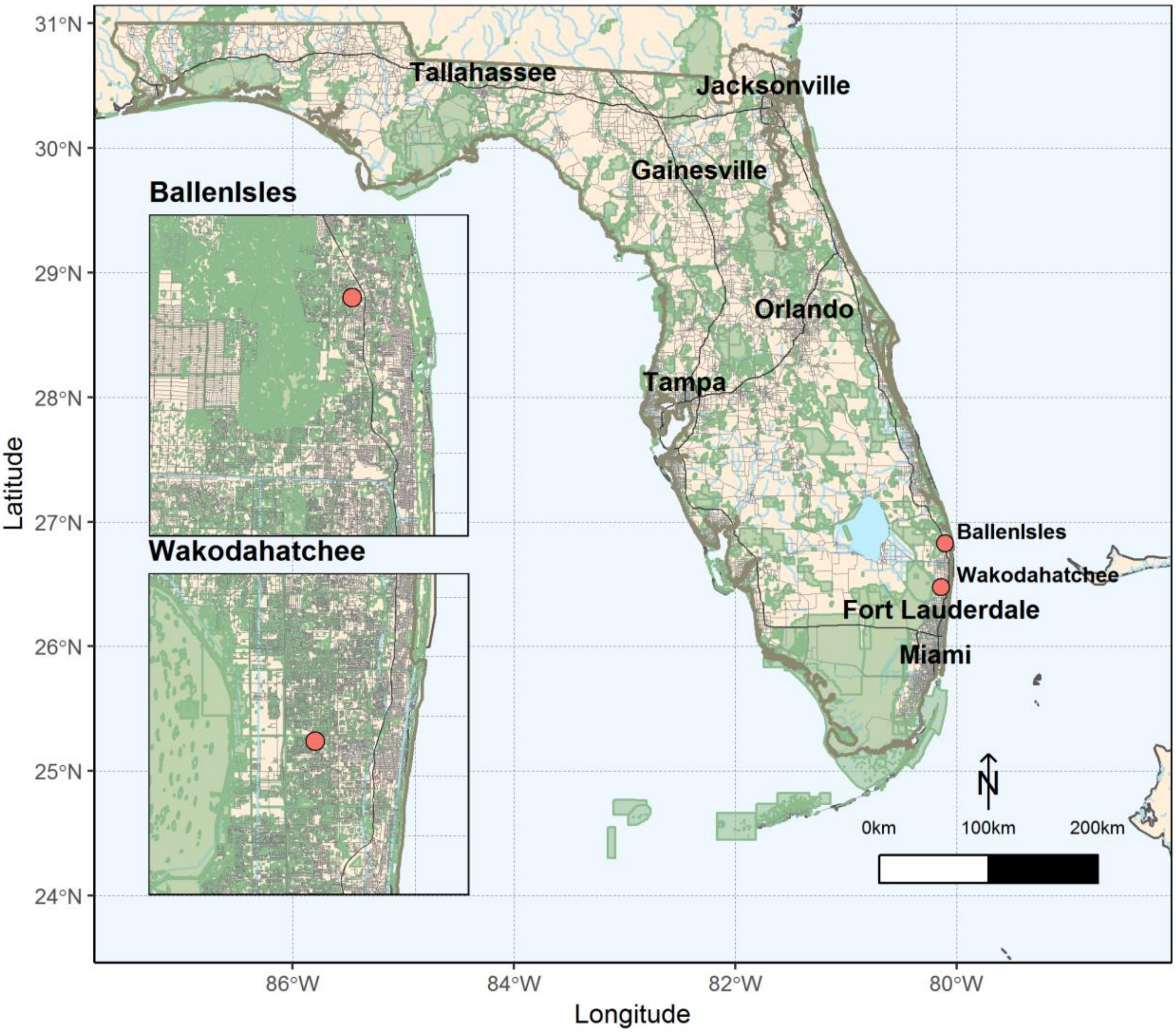
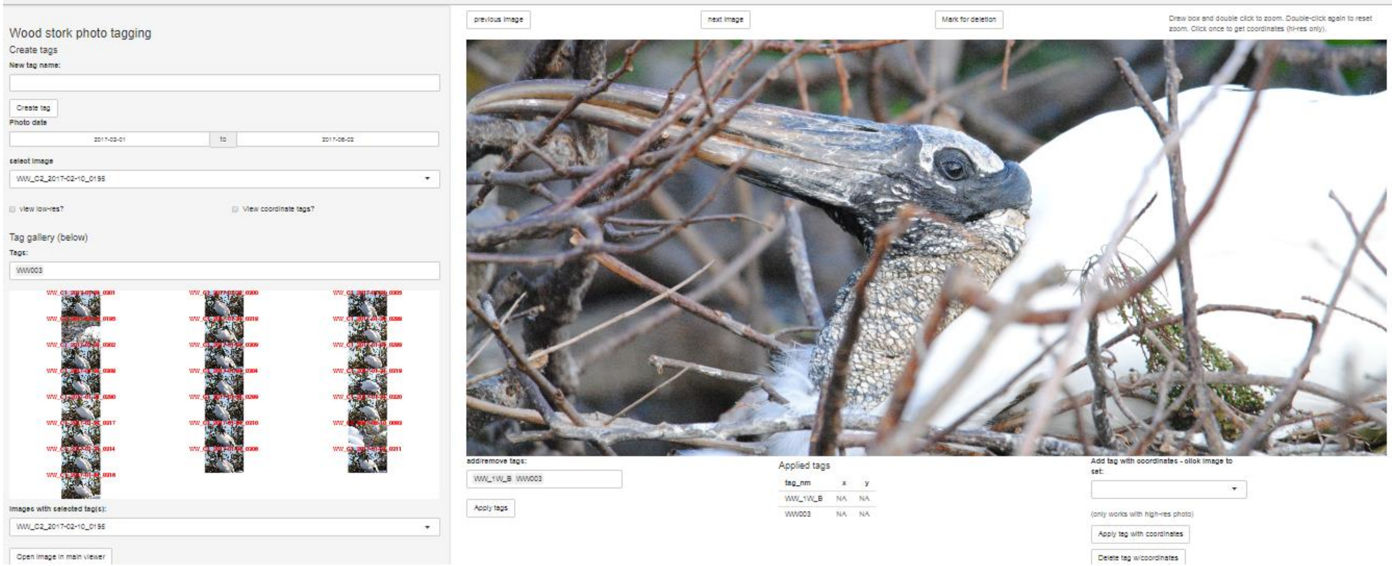
Appendices

<u>Appendix 1:</u> Location of study sites in south Florida, north of Miami and Fort Lauderdale. Protected and natural areas are presented in green; roads and interstates as grey and black lines, respectively.



Appendix 2: Screenshot of the web application accessing pictures and other information from the Wood Stork database. The application allows to identify individual Wood Stork by comparing skin patterns on profile pictures, tag individual according to their ID, nest and behavior, and locate individuals on pictures when the picture contains several individuals.



New tag name:

Photo date: 2017-02-01 to 2017-06-02

select image: WW_C2_2017-02-10_0195

☐ view low-res? ☐ View coordinate tags?

Tags: WW003

Images with selected tag(s): WW_C2_2017-02-10_0195

Draw box and double click to zoom. Double-click again to reset zoom. Click once to get coordinates (hi-res only).

add/remove tags: WW_1W_B WW003

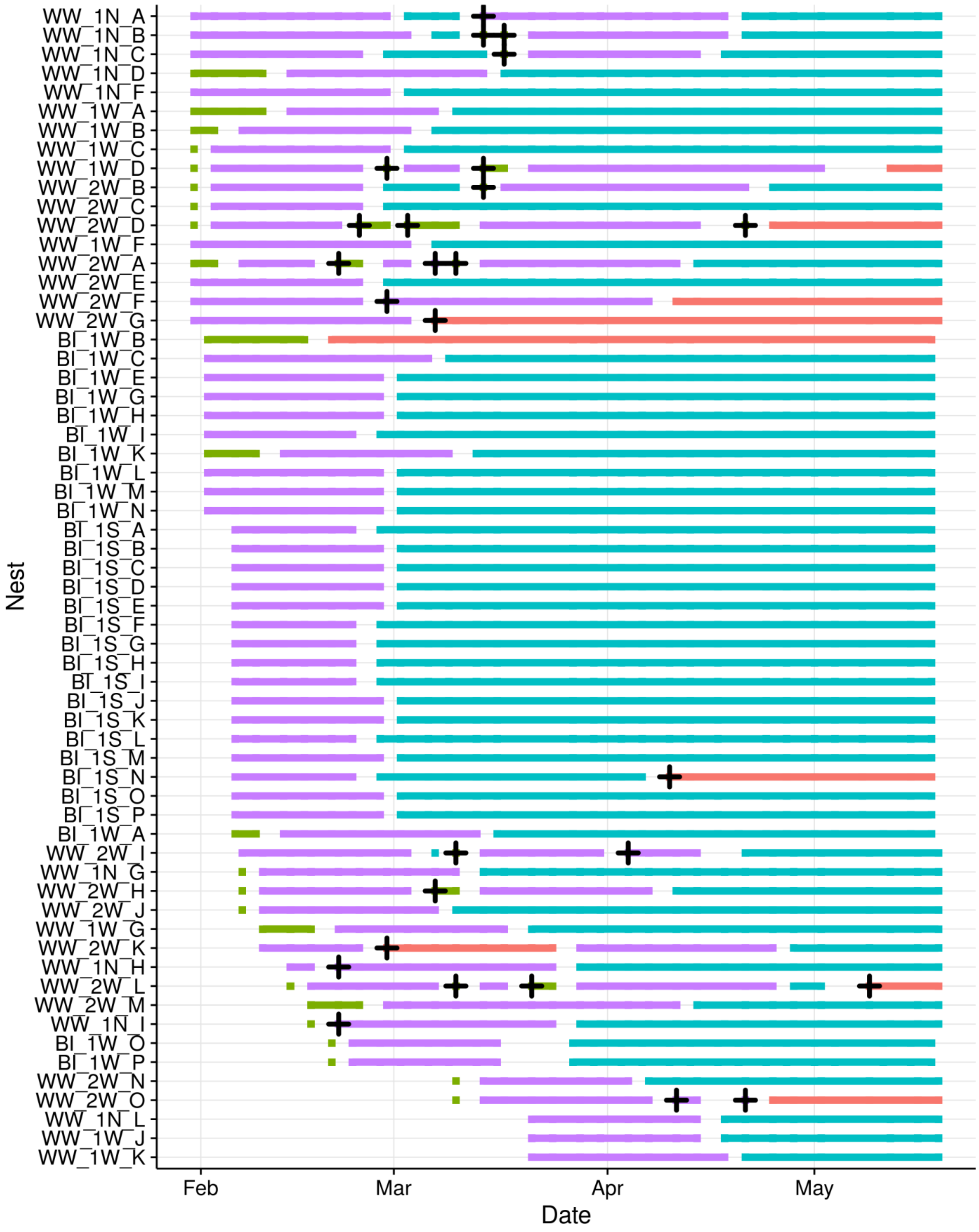
Applied tags

tag_nm	x	y
WW_1W_B	NA	NA
WW003	NA	NA

Add tag with coordinates - click image to set:

(only works with high-res photo)

Appendix 3: Evolution of nest status during the nesting season. The color indicates the phases of each pair in the nest: Building phase (green), Incubation phase (purple), Post-hatching phase (blue). Takeovers are indicated by black crosses.



Abstract

Parental care is a complex behavior, both in terms of expressed behaviors and factors driving evolution of these traits. Biparental care is predominant in birds because the presence of single parent is often not sufficient to sustain the brood. Wood Storks (*Mycteria americana*) are large wading birds dispensing biparental care and are classified as threatened in the US. In this study, I have shown that Wood Stork gradually increased the frequency, but not the duration, of foraging trips during the period of chick development. In addition, reproductive success ratio (number of hatchlings / number of fledglings) is positively influenced by the number of foraging trips during the late stage of chick development. The occurrence of "takeovers" was greater in late-breeding pairs and seemed to peak in the first few weeks of incubation. Wood Stork preferred to increase the number of foraging trips rather than their duration to meet the growing energetic demand of chicks. Finally, takeovers can affect many nests during the breeding season (30 % in my study), and a late initiation of incubation would increase this risk.

Key words: foraging, *Mycteria Americana*, nest attendance, parental care, takeover

Résumé

Le soin parental est un comportement complexe, à la fois en termes de caractéristiques et de comportements exprimés et en termes de facteurs entraînant l'évolution de ces traits. Au sein de la classe aviaire, le soin biparental est prédominant car la présence d'un seul parent n'est souvent pas suffisante pour mener la couvée à terme. Le Tantale d'Amérique (*Mycteria americana*), classé comme menacé aux États-Unis, est un grand échassier prodiguant des soins biparentaux. Mon étude sur la reproduction de cette espèce a montré une augmentation graduelle de la fréquence, mais pas de la durée, des voyages de fourragement durant la période de développement des jeunes. De plus, le ratio du succès reproducteur (nombre de jeunes post-éclosion/nombre de jeunes à l'envol) est influencé positivement par le nombre de voyages de fourragement lors de la phase tardive de développement des jeunes. L'occurrence des « takeovers » est significativement plus importante chez les couples nichant tardivement dans la saison et présente un pic durant les premières semaines de l'incubation. Le Tantale d'Amérique privilégierait l'augmentation du nombre de voyages de fourragement plutôt que la durée pour subvenir à la demande croissante de nourriture des jeunes. Enfin, le comportement de takeover peut affecter de nombreux nids dans la saison de reproduction (30 % dans mon étude) et une date tardive d'initiation de l'incubation augmenterait le risque de son occurrence.

Mots clés : fourragement, *Mycteria americana,* présence au nid, soin parental, takeover