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Effect of Foraging and Nest Defense tradeoffs on the Reproductive Success of Wood Storks (*Mycteria americana*)

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12   Running title: PARENTAL CARE IN WOOD STORKS

13   **Abstract.** —In many species of birds, parental care is provided by both parents to

14   maximize offspring survival, and there may be important trade-offs between

15   maximizing food gathering and nest protection during the nesting period. The role

16   of parental care in determining reproductive success was investigated in Wood

17   Storks (*Mycteria americana*), and specifically how the trade-off between frequency

18   and duration of foraging trips, and nest protection has contributed to the nesting

19   outcome. Parental behavior of 85 pairs of Wood Storks was monitored throughout

20   the nesting season in two breeding colonies in Palm Beach County, Florida. Wood

21   Storks have gradually increased the frequency, but not the duration, of foraging

22   trips as chicks developed. The ratio of hatchlings to fledglings was positively

23   associated with the frequency of foraging trips during late chick development. Intra-

24   specific aggressions resulting in nest takeovers have affected 32 % of the nests

25   under study. Occurrence of nest takeovers have been higher for later-breeding pairs,

26   and was happened primarily in the first few weeks of incubation, but was not

27   affected by the degree of joint nest attendance of both parents. These results

28   establish a functional link between parental effort and reproductive outcome in

29   Wood Storks, and highlight the importance of frequent foraging trips, but not nest

30   attendance, by parents.

31   **Key words.**—foraging trips, intra-specific aggressions, nest attendance, nest

32   takeover, parental care

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33   Any pre- or post-breeding investment made by a parent that increases offspring survival

34   (parental care; Trivers 1972, Westneat and Sherman 1993, Royle *et al.* 2012), may affect re-

35   productive success (Eggert *et al*. 1998). For many species of birds, including most waterbirds

36   (Del Hoyo *et al*. 1992), biparental care is the rule (> 90%; Silver *et al.* 1985, Cockburn 2006,

37   Harrison *et al.* 2009). The degree of parental care received by offspring can be crucial for their

38   survival and, as a consequence, can affect the reproductive success of the parents (Elowe and

39   Dodge 1989, Dijkstra *et al*. 1990, Boland *et al*. 1997). For instance, quality of parental care

40   (body condition of parents), instead of quality of egg (egg size), has been shown to affect chick

41   survival in Short-tailed Shearwaters (*Puffinus tenuirostris*; Meathrel *et al*. 1993).

42   Wood Stork's behavior such as incubation, brooding, number of feedings or nest protec-

43   tion has been studied in several studies (Clark 1980, Bryan and Coulter 1991, Bryan *et al*. 2005),

44   but the effect of Wood Stork's behavior on reproductive success has not been investigated yet.

45   To our knowledge, no study has quantified the direct impact of food provisioning on survival

46   of chicks in Wood Stork. In particular, altricial and semi-altricial hatchlings cannot feed them-

47   selves, yet require a copious and steady flow of nutrients to fuel rapid growth and development

48   (Schwagmeyer and Mock 2008). However, provisioning takes time and energy, and parents

49   should trade off optimal levels of offspring provisioning versus nest defense (Mutzel *et al*.

50   2013), clutch size (Dijkstra *et al*. 1990), clutch mass (Hébert and Barclay 1988), or parental

51   body condition (Erikstad *et al*. 1997). Moreno *et al*. (1999) showed that increasing the intake

52   of food positively affected reproductive success, but little is known about how the trade-off

53   between food provisioning and nest protection impacts reproductive success.

54   In Wood Storks (*Mycteria americana*), both parents provide parental care (Kahl 1962,

55   1971, US Fish and Wildlife Service 2001). Earlier studies suggest that daily care from both

56   parents is strictly necessary to ensure survival of eggs and offspring in this species (Clark 1980,

57   Bryan *et al.* 2005). Survival of nestling Wood Storks is affected by many factors, including

58   predation (Rodgers 1987), human disturbance (Bouton *et al.* 2005), intraspecific aggression

59   that can lead to nest takeover (Bryan and Coulter 1991), contamination with toxic chemicals

60   (Fleming *et al*. 1984, Burger *et al*. 1993), as well as weather conditions, such as storms associ-

61   ated with strong winds (Coulter and Bryan 1995, Bouton et *al*. 2005, Bryan and Robinette

62   2008). However, the reproductive success of Wood Stork seems to be primarily related to prey

63   availability in the environment (Ogden 1994, Griffin *et al.* 2008), which affects the ability of

64   parents to provide sufficient food to sustain the development of chicks until fledging. Wood

65   Storks feed mainly on fish (Kahl 1962, 1971, Ogden *et al.* 1976), captured in 15–50 cm deep

66   water (Coulter and Bryan 1993) using "tactolocation" (Kahl and Peacock 1963, Kahl 1964,

67   Clark 1979). This technique is extremely sensitive to variations in fish availability. Sufficient

68   rains prior to the breeding season are required to increase wetland water levels and increase

69   prey population growth, followed by decreased water levels during the nesting phase to con-

70   centrate prey and ensure efficient foraging when energetic needs are highest (Kushlan *et al*.

71   1975, Ogden and Nesbitt 1979, Beerens et *al*. 2015). In contrast, heavy rains during the breed-

72   ing season can result in colony abandonment due to dispersion of prey (Frederick and Collopy

73   1989, Ramo and Busto 1992).

74   Biparental contributions to nest protection and food provisioning by Wood Storks have

75   been confirmed in several studies (Kahl 1962, Coulter et al. 1999, Griffin et al. 2008). Wood

76   Stork parents must budget their time efficiently to provide adequate food and at the same time

77   protect their young in the first weeks after hatching, when chicks are unable to defend them-

78   selves or to thermoregulate autonomously (Bryan and Coulter 1987). In this first phase, the

79   continuous presence of a parent on the nest is necessary (Clark 1980, Bryan *et al*. 2005). After

80   three weeks, chicks exhibit a behavioral change, becoming aggressive to any approach (con-

81   specifics and other species, Kahl 1971) and are able to thermoregulate (Clark 1980). This in-

82   creased autonomy allows both parents to forage simultaneously when food requirements of the

83   chicks are at their peak, leaving the nest unattended (Kahl 1962). Nestling Wood Storks remain

84   in nests for 50 to 60 days before fledging (Kahl 1971, Coulter *et al.* 1999) and continue to return

85   to nests to be fed by their parents for another one to three weeks (Kahl 1971, Borkhataria *et al.*

86   2012).

87   The trade-off between nest attendance and food provisioning has been noted in many

88   species of birds (Komdeur and Kats 1999, Fontaine and Martin 2006, Tilgar *et al*. 2010). A key

89   assumption in this trade-off is that nest attendance is related to nest success, through several

90   mechanisms, such as direct care for chicks, and defense of nest against predators and conspe-

91   cifics (Giese 1996, Schmidt and Whelan 2005). To our knowledge, no study has investigated

92   the relationship between parental care (measured as frequency of foraging trips, their duration,

93   and nest attendance) and reproductive success in Wood Storks but has been in other wading

94   birds (Miller and Burger 1978); likewise, the importance of parental attendance during the nes-

95   tling period has been little studied in this group. Thus, our objective was to determine if parental

96   care (nest attendance and foraging behavior) varies during the nesting season and, if so, if such

97   variation affects reproductive success. We predicted that the number of parental foraging trips

98   would increase with the age of chicks, and the mean duration of foraging trips would decrease.

99   We also predicted a positive relationship between number of foraging trips and reproductive

100   success. Second, we assessed a possible relationship between the time spent by parents at the

101   nest and the occurrence of takeover events. We predicted that the percentage of time spent at

102   the nest simultaneously by both parents would reduce the likelihood of takeovers.

METHODS

103

Study areas

104

105   We collected data on parental activities of 85 pairs of Wood Storks on 61 nests (due to

106   takeovers and abandoned nests) in two colonies in Palm Beach County, Florida. We observed

107   32 nests on two islands located within the Wakodahatchee Wetlands (26°47'87"N,

108   80°14'34"W), nesting on pond apple (*Annona glabra*), dahoon holly (*Ilex cassine*), and sabal

109   palm (*Sabal palmetto*) (Bays *et al*. 2000). We also monitored 29 nests in pond apple and sabal

110   palm in the Ballenisles Country Club, situated on a single island within a golf club

111   (26°83'01"N, 80°10'91"W), located 46.6-km north of Wakodahatchee Wetlands (Fig. 1). It is

112   important to note that Palm Beach County and the large adjacent protected marsh lands (includ-

113   ing Loxahatchee National Wildlife Refuge) are a hotspot for the year-round distribution of res-

114   ident wood storks, which may indicate that foraging habitat is generally good in this area (Pi-

115   cardi *et al*. 2020). The 2017 breeding season in Palm Beach County was characterized by lower

116   precipitation (2,68 mm in January and February, 5,26 mm in March through May) than the

117   long-term average (9,33 mm for December through February 1981-2010, 12,76 mm for March-

118   May 1981-2010; data from the National Oceanic and Atmospheric Administration).

Data collection

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120   We observed breeding behavior in the two colonies from January 31st to June 2nd, 2017.

121   Two observers conducted separate two 5h-long surveys biweekly at each colony, once in the

122   morning (07:30 hr to 12:30 hr) and once in the afternoon (12:30 hr to 17:30 hr), as to homoge-

123   nize time gaps between successive surveys at a single site (every 3.5 days, Monday morning

124   and Thursday afternoon at BallenIsles, Tuesday morning and Friday afternoon at Wakoda-

125   hatchee Wetlands). At each site, two groups of nests were observed in weekly alternation by

126   both observers to prevent observer bias. Wood Stork behavior was observed using binoculars

127   (12×50) and recorded using an SLR camera with a 600-mm telephoto lens. We began data

128   collection when most pairs of Wood Storks were either building nests or beginning to incubate

129   eggs. We identified each individual Wood Stork based on unique skin patterns on their head,

130   which are individually unique (Clark 1980, Bryan and Coulter 1991). We built a photographic

131   database for individual identification, consisting of photos of the right and left profile of each

132   stork. Because Wood Storks lack evident sexual dimorphism, sexing partners of a pair was only

133   possible when we witnessed copulation (Clark 1980, Fujioka and Yamagishi 1981, Bryan and

134   Coulter 1991).

135   At the beginning of each survey, we recorded the status of each nest (construction, in-

136   cubation or post-hatching, individual parents present), took pictures of the individuals present,

137   and recorded arrivals and departures. Identification was always made later using the photo da-

138   tabase. The takeovers were either observed directly or inferred from the data showing the pres-

139   ence of different adults in the nest. A takeover can be carried out by a single individual or by a

140   pair who are seizing an already built nest. This may result in the cessation of egg incubation or

141   the death of the original pairs' chicks present in the nest at the time of the takeover. Trips were

142   categorized as foraging or gathering nest building material based on whether the parents regur-

143   gitated food to nestlings upon return, or brought back twigs and other woody material, respec-

144   tively. Trips were initially classified as unknown when parents neither fed nor carried nest ma-

145   terial when returning. We found that 96% of foraging trips (showing regurgitation) lasted more

146   than 44 min. Using that information, we categorized any unknown trips longer than 44 min as

147   foraging trips. Laying dates for each nest were estimated by back-dating from hatching dates,

148   using an average incubation period of 28 days (Rodgers and Schwikert 1997) and were matched

149   to observations of parental brooding behavior (especially sitting position). We counted hatch-

150   lings in each nest where visual counting was feasible. We estimated reproductive success at

151   each nest as the proportion of hatching chicks still alive after 8 weeks, i.e. the estimated time

152   when young birds leave the nest for the first time (Middleton and Prigoda 2001, Bryan *et al*.

153   2005). We determined early and late pairs according to their nesting date. Most pairs (48 out of

154   61) initiated nesting within the first week of study, before February 8, 2017, and were consid-

155   ered early nesters. A second wave initiated nesting between February 20, 2017, and April 21,

156   2017 and were considered late nesters.

Analytical Methods

Changes in frequency and duration of foraging trips

159   We modeled both frequency and duration of foraging trips as non-linear functions of

160   weeks since hatching using generalized linear mixed models (Mirman 2014). The overall shape

161   of the curve was captured with inclusion of orthogonal polynomials on time up to the fourth

162 order, with individual-within-nest random effects on all terms (for frequency only; for the du-

163 ration analysis, the use of complete trips with known time of departure and arrival limited the

164 sample size, and the estimation of random effects was not possible). Using a subset of individ-

165 uals of known sex, sex differences were tested with the inclusion of an additive and multiplica-

166 tive fixed effect of sex. Similarly, we included an additive and multiplicative fixed effect of the

167 calendar date of nest initiating to test its effect on frequency and duration of foraging trip.

168 Effect of frequency of foraging trips on reproductive success ratio

169 The effect of frequency of foraging trips on reproductive success was then assessed us-

170 ing a logistic regression on the number of successes (fledglings) over failures (hatchlings that

171 did not survive until fledging) in each nest. Fixed effects of the frequency of foraging trips

172 during the early pre-flight stage (weeks 1–4) and during the late pre-flight stage (weeks 5–8)

173 were included in the regression, after checking for their correlation. We have not reported re-

174 sults for the post-flight stage because the data were not sufficient to constitute a robust data set.

175 In fact, at the end of the young's development (between 9 and 12 weeks), parents return very

176 little to the nest to feed them. It happened several times that the parents did not return to the

177 nest during the 5.5 hours of observation.

178 Nest attendance and risk of takeover

179 We fit semi-parametric proportional hazards (SPPH) models to the time spent by parents

180 at the nest prior to takeovers, expressed either as a function of calendar time, or time within the

181 nest cycle. The instantaneous risk of successful takeover of a nest at a given week was modeled

182 as a function of the baseline hazard experienced by all individuals, and the proportion of time

183 with at least one adult or two adults present at the nest during the week. In the semi-parametric

184 approach, weak assumptions about the baseline hazard are made, allowing the estimation of the

185 relative risk of takeover. Covariate effects are then estimated using a partial likelihood that does

186 not require estimating the baseline hazard.

187 All statistical analyses were performed in the software R 3.3.0 (R Core Team 2017)

188 using notably the packages "lme4" (version 1.1.13; Bates *et al.* 2015), "survival" (version

189 2.40.1; Therneau and Grambsch 2000), and "cowplot" for graphs (version 0.7.0; Wilke 2016).

6

RESULTS

Wood Stork monitoring

Observations from the two sites were similar. For instance, comparing the two sites we obtained an average foraging rate of 0.243 h^{-1} for Ballenisles Country Club versus 0.239 h^{-1} for Wakodahatchee Wetlands. Moreover, the pairs with the highest chick survival were those with the highest mean frequency of foraging trips per hour in each site. We thus pooled both colonies to increase robustness of our results. Between January 31st and June 2nd 2017, we monitored 61 nests (29 in BallenIsles, and 32 in Wakodahatchee Wetlands), corresponding to 85 nesting attempts from individually identifiable pair of Wood Stork (with sex identified for individuals of 71 pairs). Of these nest attempts, 27 were taken over by another pair, five were abandoned, and 53 either succeeded or were still active at the end of data collection (Fig. 2). Among surviving nests, we were able to track the fate of chicks until fledging for 29 nest attempts (see Table 1). For the other nest attemps, we were not able to track the fate of chicks until fledging due to either takeover, death of chicks, abandoned nest or the end of the observation period. We found an average of 3.00 ± 0.46 SD hatchlings per nest, and an average of 2.59 ± 0.57 SD chicks fledged per nest.

Changes in frequency and duration of foraging trips

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), whereas adding a cubic or quartic term did not further 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 quadratic model as a baseline, model selection reaeled that an additive or multiplicative effect either sex (Table 2B) or initiation date (Table 2C) did not significantly improve the fit (Table 2B). The model including the effect of first- and second-order polynomials was kept for the rest of analyses (Table 3). This model showed a significant effect of the first-order orthogonal polynomial term (0.225 ± 0.06, $t_{910} = 13.501$, $P < 0.001$; Table 3) demonstrating a positive linear relationship between the frequency of foraging trips and the progression of chick development (Fig. 3A).

Adding orthogonal polynomials 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 close to statistical significance ($F_{1,155} = 3.612$, $P = 0.059$; Table 4A). We thus simplified the baseline foraging duration 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

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222 showed that the additive or multiplicative effect of sex (Table 4B) and initiation date (Table

223 4C) did not significantly improve the fit. The simple linear model including no effect of sex or

224 start time of nesting was thus kept for the rest of analyses, and indicated a weak trend of de-

225 creasing duration of foraging trips through time since hatching (-2.629 ± 1.388, $t_{27} = -1.893$,

226 $P = 0.060$; Table 5; Fig. 3B).

Effect of frequency of foraging trips on reproductive success

228 We divided the post-hatching phase into three stages: early pre-flight (weeks 1–4 post-

229 hatching), late pre-flight (weeks 5–8) and post-flight (weeks 9–12; Clark 1980). The frequency

230 of foraging trips increased during each stage of chick development. However, the effect of the

231 frequency of foraging trips on reproductive success was not significant during the early pre-

232 flight stage (weeks 1–4; $Z = 1.025$; $P = 0.306$; Table 6). Frequency of foraging trips during the

233 late pre-flight stage had a significant positive effect on reproductive success ($Z = 2.929$; $P =

234 0.003$; Table 6; Fig. 4). The frequency of foraging trips had no effect on the absolute number

235 of fledglings ($Z = 1.035$; $P = 0.438$). Pairs with the highest chick survival ($P = 1$) were those

236 with the highest mean frequency of foraging trips per hour (0.25 to 0.35 h^{-1}), whereas pairs with

237 the lowest chick survival ($P = 0.5$) had the lowest mean frequency of foraging trips per hour

238 (0.12 to 0.16 h^{-1}). The mean frequency of foraging trips during the early and late pre-flight

239 stages were not correlated ($r = 0.216$, $t_{27} = 1.148$, $P = 0.261$).

Nest attendance and risk of takeover

241 Both adults of each pair were simultaneously present at nests more than half of the time

242 during nest building and the first week of incubation, but, this proportion declined rapidly dur-

243 ing incubation (Fig. 5A). Until the beginning of the early pre-flight stage, at least one adult was

244 always constantly at the nest. Then, the presence of even one adult gradually decreased, reach-

245 ing a minimum of 10% of the time at the end of the nesting season (Fig. 5A). In our study, 32%

246 of nests experienced a takeover. Of the 27 takeovers, the vast majority took place in Wakoda-

247 hatchee Wetlands (26) vs. only 1 in Ballen Isles. Most takeovers occurred between February 13

248 to March 19 2017 (Fig. 5B). However, we found that the amount of time with presence of at

249 least one parent at the nest did not significantly affect risk of successful takeovers ($e^{\beta} = 1.030$,

250 $Z = 1.289$; $P = 0.197$; Table 7), whereas a higher presence of both parents at the nest had a

251 significant positive effect on the risk of takeover ($e^{\beta} = 1.017$; $Z = 2.506$; $P = 0.012$; Table 7).

252 Similarly, the date of initiation of incubation had a positive effect on the risk of takeovers, with

253 later initiation dates associated with higher risk ($e^{\beta} = 2.135$; $Z = 1.971$; $P = 0.048$; Table 7; Fig.

254 5C).

8

DISCUSSION

255   We found that the mean frequency of foraging trips per hour showed a gradual increase

256 in time with the developmental stage of chicks. However, our sample of chicks in the post-

257 flight stage was small and highly variable among different pairs, thus limiting our inference

258 during the final stage. The duration of foraging trips was not influenced by the developmental

259 stage of chicks. These results are in general agreement with those of previous studies of Wood

260 Storks (Clark 1980, Bryan *et al.* 1995, 2005). Parents meet the increased energetic needs of

261 chicks (Kahl 1962) by increasing the number rather than the duration of foraging trips (Bryan

262 *et al.* 1995). During the post-hatching phase, the mean frequency of foraging trips per hour and

263 their duration were not different between the sexes, and were not related to the onset date of

264 incubation. Whether or not the duration of foraging trips is always stable as chicks grow is

265 unclear, but may depend on the mosaic of wetland conditions in the area surrounding at colony

266 (Coulter and Bryan 1993, Bryan *et al.* 1995). The dry season was not interrupted by major

267 rainfall events that could reverse gradual water drydown, and this resulted in good conditions

268 for wood stork foraging in our study area (Kushlan 1986). However, precipitation in summer

269 2016 were lower (7,7 mm) than the long-term average (22,01 mm) in Palm Beach County. High

270 water levels in the prior non-breeding season promote growth of fish populations (DeAngelis

271 et al. 2010, Botson et al. 2016), so it is possible that the low levels observed in 2016 prevented

272 foraging conditions from reaching optimality in 2017, despite the favorable trends of water

273 recession during the breeding season.

274   We found that the mean rate of foraging trips in the late pre-flight stage, but not in the

275 early pre-flight stage, affected the proportion of chicks that fledged. Although our results

276 showed that pairs with the highest chick survival were those with the highest mean frequency

277 of foraging trips per hour and that pairs with the lowest chick survival had the lowest mean

278 frequency of foraging trips per hour, it is important to note the possible circularity of this rela-

279 tionship: in fact, one could argue that pairs that reached the late pre-flight stage with an already

280 reduced brood size consequently decreased the frequency of trips due to reduced demands from

281 the offspring, rather than the other way around. However, our results show that the relationship

282 between reproductive success and frequency of foraging trips is independent of the absolute

283 number of fledglings. For example, pairs with two successful chicks but low fledging success

284 had either higher (0.23–0.28 h^{-1} for success ratio of 0.67, see Fig. 2) or lower (0.13–0.16 h^{-1} for

285 success ratio of 0.5, see Fig. 4) foraging trip frequency than those with 100 % success ratio

287 (0.17–0.23 h^{-1}, see Fig. 4). If the absolute number of chicks was driving the frequency of for-

288 aging trips, we would expect the same frequency for an equal number of chicks independently

289 from the initial brood size. This result supports an effect of foraging trip frequency in determin-

290 ing chick survival ratio, and not vice-versa. Because we found no effect of the frequency of

291 foraging trips on the absolute number of fledglings, fledging success is apparently determined

292 by other factors, such as mortality related to predation, sibling competition, or disturbance, as

293 well as factors affecting clutch size (Burger 1982, Rodgers 1987, Bouton *et al.* 2005).

294   Takeover behavior appears to be widespread in Wood Storks, where it may affect more

295 than a third of pairs in a colony (Bryan and Coulter 1991). In our study, 32% of nests experi-

296 enced a takeover. The risk of a takeover was more than double for late pairs (nest initiation after

297 February 13th). The lower occurrence of takeovers for early pairs could be explained by better

298 intrinsic characteristics of individuals (Johnson and Kermott 1990) such as larger size, higher

299 energy reserves, greater aggressiveness, or higher social status (i.e. dominance hierarchy rank).

300 We also found that the time of simultaneous nest attendance by both parents did not reduce the

301 occurrence of takeovers. On the contrary, and surprisingly, pairs with greater nest attendance

302 times by both individuals had a greater chance of undergoing a takeover. Because Bryan and

303 Coulter (1991) found that all takeovers occurred when a single individual was present at a nest,

304 we expected that pairs that spent more time together at the nest would have a lower chance of

305 getting their nest taken over, but, instead, we found that the presence of both individuals was

306 associated with a greater risk of undergoing a takeover. Pairs may increase joint attendance

307 when their perceived risk of attack is greater, but we have no data to test this possible explana-

308 tion. In any case, increased parental attendance did not result in reduced risk of nest failure,

309 suggesting that there may not be a clear trade-off between attendance and time spent foraging.

310 Perhaps attendance of both parents at the nest does not provide appropriate protection against

311 takeovers, and body condition of parents may be a determining factor as shown in the study by

312 Meathrel *et al.* (1993) in Short-tailed Shearwaters.

313   Wood Storks have long breeding cycles (~110 days), and are often limited by food avail-

314 ability at the end of the dry season (Kushlan *et al.* 1975). Our results suggest that the frequency

315 of foraging trips during the late pre-flight stage is positively associated with the reproductive

316 success of Wood Storks. To our knowledge, this is the first time a link is established between

317 parental effort and reproductive success for this species. Moreover, our findings highlighted an

318 important mechanism of nest failure, nest takeovers, and that the risk associated with it varies

319 throughout the season. Thus, in addition to constraints related to seasonal water level fluctua-

320 tions, a late nesting initiation can be associated to low reproductive success due to a higher

10

321 probability of takeover events. It is important to point out that we have one season of data and

322 that the reproductive success of Wood Stork is primarily related to prey availability in the en-

323 vironment (Ogden 1994, Griffin *et al.* 2008). This food availability is important for the devel-

324 opment of chicks until fledging. Thus, a study carried out over several breeding seasons in the

325 same location could provide more accurate breeding estimates as foraging conditions are a dy-

326 namic system component.

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Supplemental Material

484

485 **Plate 1.** An adult Wood Stork (*Mycteria americana*) attending its nest, with a three-weeks old
486 nestling. Study of nest attendance over time showed it had not effect on the risk of conspecific
487 taking over the nest, and ultimately on nest success.

488 Tables

489 **Table 1. Reproductive success for 29 Wood Stork (*Mycteria Americana*) nests with known**
490 **outcome in south Florida: Number of nests broken down by the number of chicks per nest**
491 **at the time of hatching (rows) and at the time of fledging (columns).**

# Hatchlings \ # Fledgings	1	2	3	Total
2	1	2	0	3
3	0	5	18	23
4	0	3	0	3
Total	1	10	18	29

492 **Table 2. Model selection for frequency of foraging trips by Wood Storks (*Mycteria Amer-***
493 ***icana*). *K* is the number of parameters in the model; AIC the Akaike Information Crite-**
494 **rion, LL the log-likelihood, and χ^2, df and Pr($>\chi^2$) indicates the statistic, the associated**
495 **degrees of freedom and *p*-value for the comparison between each model and the previous**
496 **one. The selected model is indicated in bold.**

General shape

Model	K	AIC	LL	χ^2	df	Pr($>\chi^2$)
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

Sex effect

Model	K	AIC	LL	χ^2	df	Pr($>\chi^2$)
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

Effect of the start date of nesting

Model	K	AIC	LL	χ^2	df	Pr($>\chi^2$)
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

497 **Table 3. Coefficients and their significance of the best model for the frequency of foraging**
498 **trips during the post-hatching phase in Wood Stork (*Mycteria Americana*).**

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

499 **Table 4. Model selection for duration of foraging trips by Wood Storks (*Mycteria Ameri-***
500 ***cana*). SSR and SSE are the residual and explained sums of squares, respectively with**
501 **their associated degrees of freedom, and *F*, and Pr(>*F*) indicate the statistic and *P*-value**
502 **for the comparison between each model and the previous one. The selected model is indi-**
503 **cated in bold.**

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

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

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

504 **Table 5. Coefficients and their significance of the best model for the duration of foraging**
505 **trips during the post-hatching phase in Wood Stork (*Mycteria Americana*).**

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

506 **Table 6. Coefficients and their significance of the logistic model for reproductive success**
507 **ratio in Wood Stork (*Mycteria Americana*).**

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

508 **Table 7. Coefficients and their significance of the semi-parametric proportional hazards**
509 **(SPPH) model applied to the risk of takeovers of Wood Stork (*Mycteria Americana*) nests.**
510 **Exponentiated coefficients can be interpreted as multiplicative effects on the hazard, i.e.**
511 **the instantaneous risk of takeover, holding other covariates constant. For instance, late**
512 **starters have a risk more than twice as high as 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

22

Figure captions

Fig. 1. Location of study sites in south Florida, north of Miami and Fort Lauderdale. Protected and natural areas are presented in light gray; roads and interstates as grey and black lines, respectively.

Fig. 2. Evolution of nest status during the nesting season in Wood Stork (*Mycteria Americana*) (*n* = 61). The color indicates the phases of each pair in the nest: Building phase (stripped light gray), Incubation phase (dark gray), Post-hatching phase (light gray), Abandon (stripped dark gray). All 27 takeovers are indicated by black crosses.

Fig. 3. Frequency (A) and duration (B) of foraging trips through time during the post-hatching phase in Wood Stork (*Mycteria Americana*) (*n* = 157, r^2 = 0,22 and r^2 = 0,02 respectively). Point represent average values for each week since hatching ± SE, and the light gray line represents the best model fit (see text for details).

Fig. 4. Reproductive success ratio as a function of frequency of foraging trips in late pre-flight stage in Wood Stork (*Mycteria Americana*) (*n* = 29, r^2 = 0,43). The color of dots indicates the number of fledglings in each nest (diamonds = 3; crosses = 2; circle = 1) and the blue line indicates the logistic fit (with 95 % confidence interval).

Fig. 5. (A) Nest attendance by adult Wood Storks (*Mycteria Americana*) through time (*n* = 79 pairs). The color indicates nest attendance of two adults (dark gray), one adult (light gray) or no adults (stripped light gray). B: building phase; I: incubation phase; H: post-hatching phase. The average fledge age is between 50 to 60 days (Kahl 1971, Coulter *et al.* 1999, Bryan *et al.* 2005). (B) Kaplan-Meier survival curve (with confidence interval) for the risk of nest takeovers in 79 Wood Stork nests as a function of the week of the year (*n* = 79 pairs), or (C) week since start of incubation (*n* = 79 pairs). Colors further distinguish between early pairs (dashed lined, top), and late pairs (dotted line, bottom).
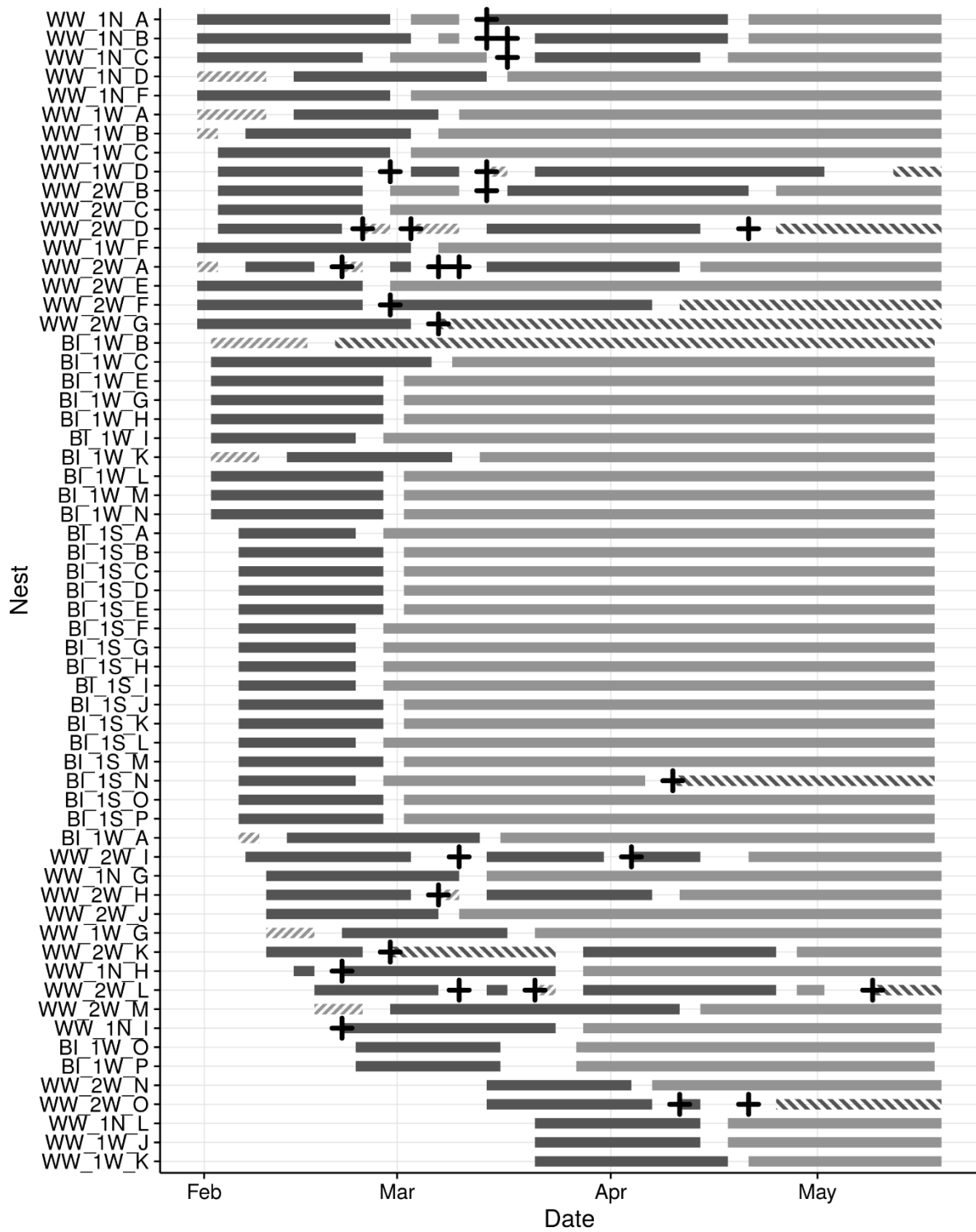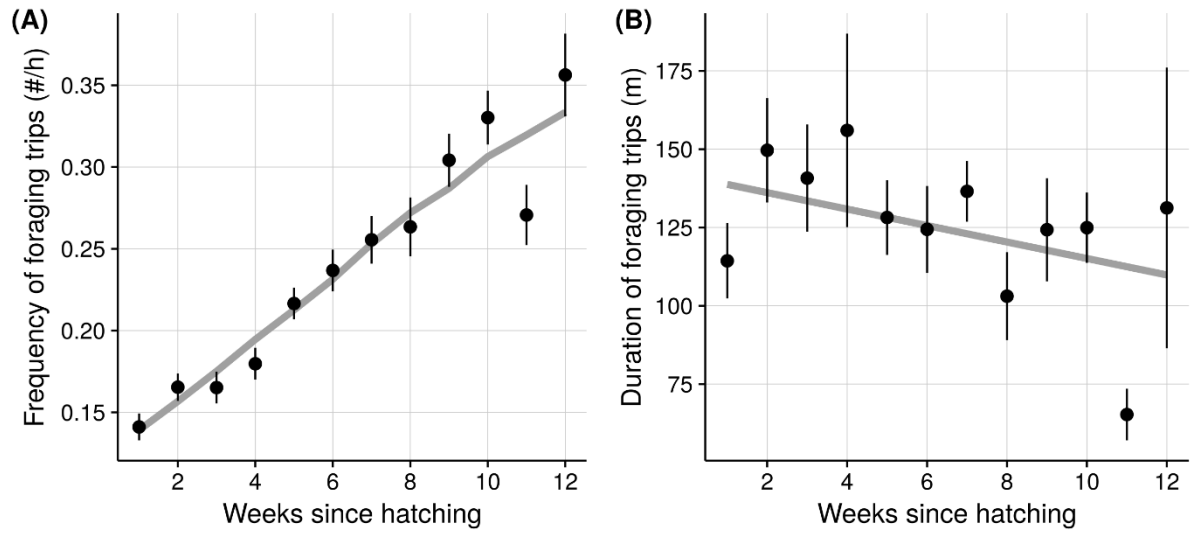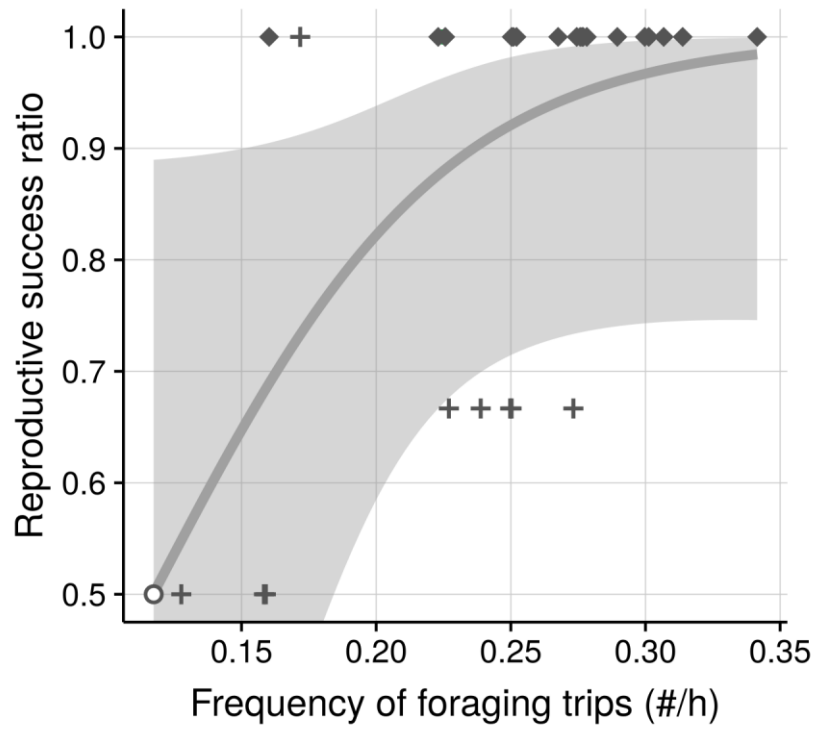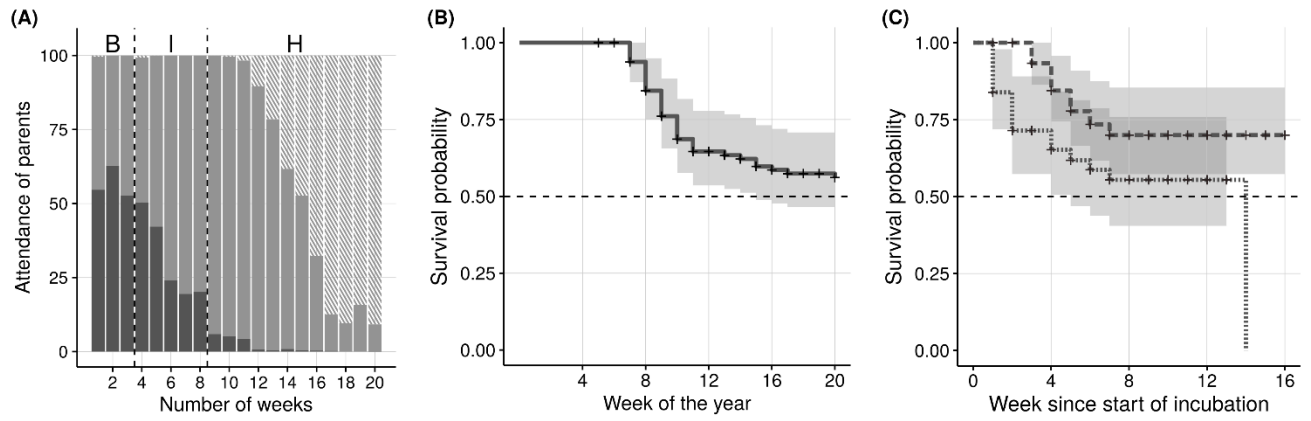
537 Figures

538 Figure 1
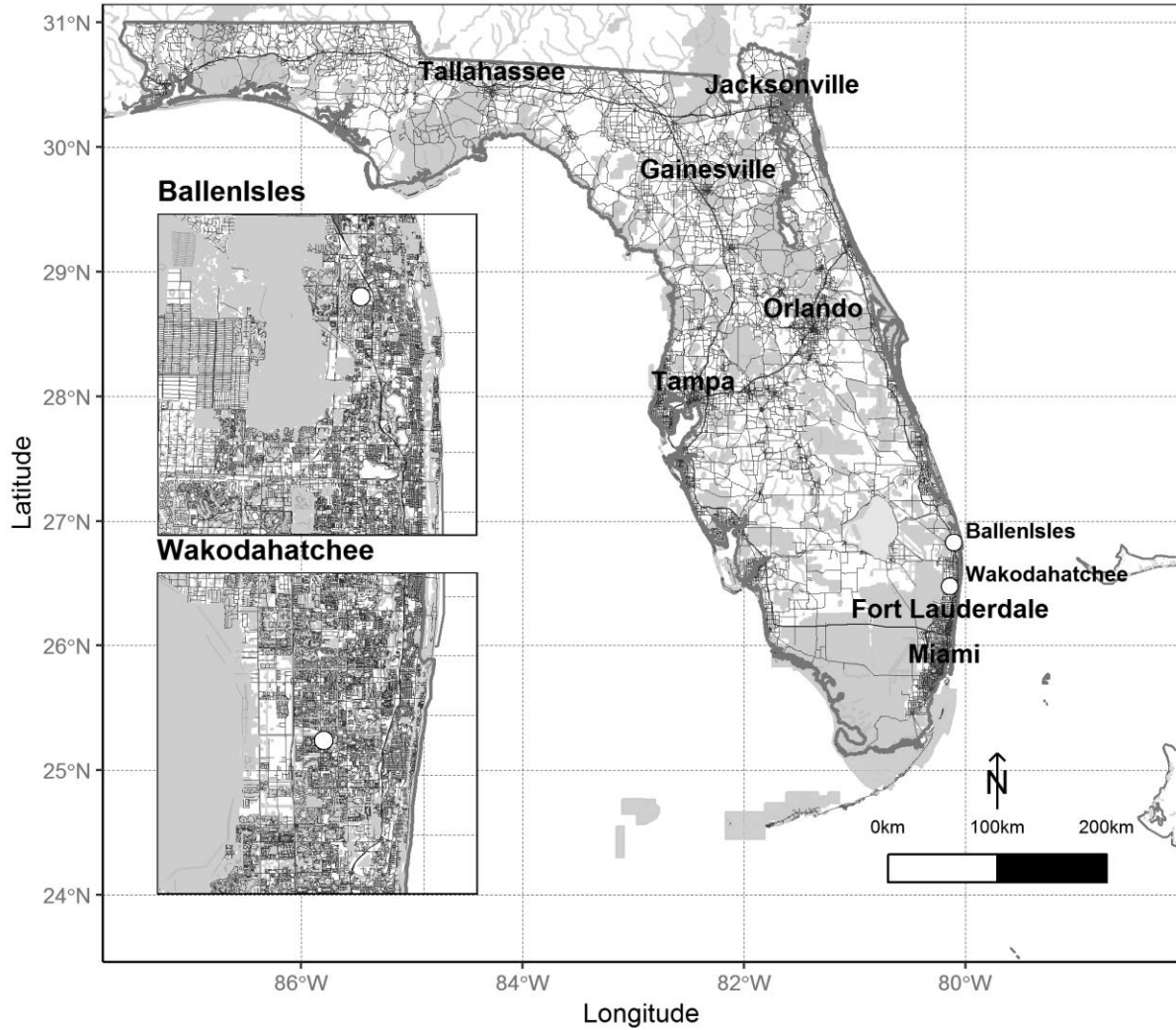
539   Figure 2

540   Figure 3

541   Figure 4

542   Figure 5

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Plate 1.