Running title: Parental care in Wood Storks

EFFECT OF PARENTAL CARE ON REPRODUCTIVE SUCCESS IN WOOD STORKS (*MYCTERIA AMERICANA*)

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Abstract

In many birds, parental care is carried out by both parents to maximize offspring survival, and there may be important trade-offs between maximizing food gathering and nest protection during the nesting period. We investigated the role of parental care in determining reproductive success of Wood Storks (*Mycteria americana*), and evaluated how the trade-off between frequency and duration of foraging trips, and nest protection contribute to the nesting outcome. We monitored parental behavior in 85 Wood Stork pairs throughout the nesting season in two breeding colonies in Palm Beach County, Florida. Wood Storks gradually increased the frequency, but not the duration, of foraging trips as chicks developed. The ratio of hatchlings to fledglings was positively associated with the frequency of foraging trips during late chick development. Intra-specific aggressions resulting in nest takeovers affected 33 % of the nests in our study. Occurrence of nest takeovers was higher for later-breeding pairs, and happened primarily in the first few weeks of incubation, but was not affected by the degree of joint nest attendance of both parents. Our results establish a functional link between parental effort and reproductive outcome in Wood Storks, and highlight the importance of frequent foraging trips, but not nest attendance, by parents.

Keywords: foraging trips · intra-specific aggressions · nest attendance · nest takeover · parental care

Introduction

Any pre- or post-breeding investment made by a parent that increases offspring survival ("Parental care", Trivers 1972, Westneat and Sherman 1993, Royle *et al*. 2012), may affect reproductive success (Eggert *et al*. 1998). In the overwhelming majority of birds biparental care is the rule (> 90 %; see; Silver *et al.* 1985, Cockburn 2006, Harrison *et al.* 2009). The degree of parental care received by offspring can turn out to be crucial in their survival, and as a consequence, affects reproductive success of the parents (Elowe and Dodge 1989, Dijkstra *et al*. 1990, Boland *et al*. 1997). For instance, quality of parental care (body condition of parents), instead of quality of egg (egg size) has been shown to affect chick survival in Short-tailed Shearwaters, *Puffinus tenuirostris* (Meathrel *et al*. 1993).

To our knowledge however, no study has quantified the direct impact of food provisioning on survival of chicks in Wood Stork. In particular, altricial and semi-altricial hatchlings cannot feed themselves, yet require a copious and steady flow of nutrients to fuel rapid growth and development (Schwagmeyer and Mock 2008). However, provisioning takes time and energy, and parents should trade off optimal levels of offspring provisioning versus nest defense (Mutzel *et al*. 2013), clutch size (Dijkstra *et al*. 1990), clutch mass (Hébert and Barclay 1988), food availability (Schwagmeyer and Mock 2008), their own body condition (Erikstad *et al*. 1997), or even their age (Clutton-Brock 1984). Moreno *et al*. (1999) showed that increasing the intake of food positively affected reproductive success, but little is known about how the trade-off between food provisioning and nest protection impacts reproductive success.

In Wood Storks (*Mycteria americana*), parental care is carried out by both parents (Kahl 1962, 1971, US Fish and Wildlife Service 2001). Earlier studies suggest that daily care from both parents is strictly necessary to ensure survival of eggs and offspring in this species (Clark 1980, Bryan *et al*. 2005). Survival of Wood Stork nestlings is affected by many factors such as predation (Rodgers 1987), human disturbance (Bouton *et al.* 2005), intraspecific aggression that can lead to nest takeover (Bryan and Coulter 1991), contamination with toxic chemicals (Fleming *et al.* 1984, Burger *et al.* 1993), as well as weather conditions, such as storms associated with strong winds (Coulter and Bryan 1995, Bouton et *al*. 2005, Bryan and Robinette 2008). However, Wood Stork reproductive success seems to be mostly related to prey availability in the environment (Ogden 1994, Griffin *et al.* 2008), which affects the ability of parents to provide sufficient food to sustain the development of chicks until fledging. Wood Storks feed mainly on fish (Kahl 1962, 1971, Ogden *et al.* 1976), captured in 15–50 cm deep water (Coulter and Bryan 1993) using a "tactolocation" (Kahl and Peacock 1963, Kahl 1964,

Clark 1979). This technique is extremely sensitive to variations in fish availability. Sufficient rains prior to the breeding season are required to increase wetland water levels and increase prey population growth, followed by decreased water levels during the nesting phase to concentrate prey and ensure efficient foraging when energetic needs are highest (Kushlan *et al*. 1975, Ogden and Nesbitt 1979, Beerens et *al*. 2015). In contrast, heavy rains during the breeding season can result in colony abandonment due to dispersion of prey (Frederick and Collopy 1989, Ramo and Busto 1992).

Biparental contributions to nest protection and food provisioning in Wood Storks has been confirmed in several studies (e.g. Kahl 1962, Coulter et al. 1999, Griffin et al. 2008). Wood Stork parents must budget their time efficiently in order to provide adequate food and at the same time protect their young in the first weeks after hatching, when chicks are unable to defend themselves or to thermoregulate autonomously (Bryan and Coulter 1987). In this first phase, the continuous presence of a parent on the nest is necessary (Clark 1980, Bryan *et al*. 2005). After three weeks, chicks exhibit a behavioral change, becoming aggressive to any approach (conspecifics and other species, Kahl 1971) and become able to thermoregulate by themselves (Clark 1980). This increased autonomy allows both parents to forage simultaneously when food requirements of the chicks are at their peak, leaving the nest unattended (Kahl 1962). Wood Stork nestlings remain in the nest for 50 to 60 days before fledging (Kahl 1971, Coulter *et al.* 1999) and continue to return at the nest to be fed by their parents for another 1 to 3 weeks (Kahl 1971, Borkhataria *et al.* 2012).

The trade-off between nest attendance and food provisioning has been noted in many avian species (Komdeur and Kats 1999, Fontaine and Martin 2006, Tilgar *et al*. 2010). A key assumption in this trade-off is that nest attendance is related to nest success, through several mechanisms, such as direct care for chicks, and defense of nest against predators and conspecifics (Giese 1996, Schmidt and Whelan 2005). To our knowledge, no study has investigated the relationship between parental care (measured as frequency of foraging trips, their duration, and nest attendance) and reproductive success in Wood Storks or other wading birds (Miller and Burger 1978); likewise, the importance of parental attendance during the nestling period has been little studied in this group. Here, we investigated whether parental care (nest attendance and foraging behavior) varies during the nesting season and whether such variation affects reproductive success. We predicted that the number of parental foraging trips would increase with the age of chicks (P1a), while the mean duration of foraging trips decreases (P1b). We also predicted a positive relationship between number of foraging trips and

reproductive success (P2). Second, we assessed a possible relationship between the time spent by parents at the nest and the occurrence of takeover events. We predicted that the percentage of time spent at the nest simultaneously by both parents reduces the occurrence of takeovers (P3).

Methods

Study areas

We collected data on parental activities of 85 Wood Stork pairs nesting in two colonies located in Palm Beach County, Florida. We observed 32 nests on two islands located within the Wakodahatchee Wetlands (26°47'N, 80°14'W), nesting on pond apple (*Annona glabra*), dahoon holly (*Ilex cassine*), and sabal palm (*Sabal palmetto*) (Bays and al. 2000). We also monitored 29 nests in pond apple and sabal palm in the Ballenisles Country Club, situated on a single island within a golf club (26°83'N, 80°11'W), 46.6-km North of Wakodahatchee Wetlands (See Supporting Online Information Appendix S1).

Data collection

We observed breeding behavior in the two colonies from January 31st to June 2nd, 2017. Two observers performed two 5h-long surveys biweekly at each colony, once in the morning (7:30 a.m. to 12:30 p.m.) and once in the afternoon (12:30 p.m. to 5:30 p.m.), as to homogenize time gaps between successive surveys at a single site (every 3.5 days, Monday morning and Thursday afternoon at BallenIsles, Tuesday morning and Friday afternoon at Wakodahatchee Wetlands). At each site, two groups of nests were observed in weekly alternation by both observers to prevent observer bias. Wood Stork behavior was observed using binoculars (12×50) and recorded using an SLR camera with a 600 mm telephoto zoom lens. We began data collection when most Wood Stork pairs were either building their nest or beginning to incubate eggs. We identified each individual Wood Stork based on skin patterns on their head, which are individually unique (Clark 1980, Bryan and Coulter 1991). We built a photographic database for individual identification, composed by a picture of the right and left profile of each stork. 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).

At the beginning of each survey, we recorded the status of each nest (construction, incubation or post-hatching, individual parents present), took pictures of the individuals present and recorded arrivals and departures. Identification was always made later through the use of the

photo database. Trips were categorized as foraging or gathering nest building material based on whether the parents regurgitated food to nestlings upon return, or brought back twigs and other woody material, respectively. Trips were initially classified as unknown when parents neither fed nor carried nest material when returning. We found that 96% of foraging trips (showing regurgitation) last longer than 44 minutes. Using that information, we categorized any unknown trips longer than 44 minutes as foraging trips. Laying dates in each nest were retrospectively estimated from hatching dates, using an average incubation period of 28 days (Rodgers and Schwikert 1997) and were matched to observation of parental behavior (especially sitting position) in the nest for brooding. We counted hatchlings in each nest where visual counting was feasible. We estimated reproductive success at each nest as the proportion of hatching chicks still alive at time that young birds leave the nest for the first time (Middleton and Prigoda 2001).

Analysis

Changes in frequency and duration of foraging trips

We modeled both frequency and duration of foraging trips as a non-linear function of weeks since hatching using generalized linear mixed models (Mirman 2014). 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 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 possible). 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, we included an additive and multiplicative fixed effect of the calendar date of nest initiating to test its effect on frequency and duration of foraging trip.

Effect of frequency of foraging trips on reproductive success ratio

The effect of frequency of foraging trips on reproductive success was then assessed using a logistic regression on the number of successes (fledglings) over failures (hatchlings that did not survive until fledging) in each nest. Fixed effects 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.

Nest attendance and risk of takeover

We fit semi-parametric proportional hazards (SPPH) models to the time spent by parents at the nest prior to takeovers, expressed either as a function of calendar time, or time within the nest

cycle. The instantaneous risk of successful 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 "lme4" (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).

Results

Wood Stork monitoring

Between January 31st and June 2nd 2017, we monitored a total of 61 nests (29 in BallenIsles, 32 in Wakodahatchee Wetlands), corresponding to 85 nesting attempts from individually identifiable Wood Stork pairs (71 of which were further sexed). Of these nest attempts, 28 underwent successful takeover by another pair, 4 were abandoned, and 53 had either succeeded or were still active at the end of data collection. Among the surviving nest, we were able to track the fate of chicks until fledging for 29 nests (see Table 1). We found an average of 3.00 (± SD = 0.46) hatchlings per nest, and an average of 2.59 (± SD = 0.57) 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), 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 quadratic model as a baseline, model selection then showed that an additive or multiplicative effect of sex (Table 2B) or of 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 highly 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. 1A).

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 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 showed that additive or multiplicative effect of sex (Table 4B) or initiation date (Table 4C) did not significantly improve the fit. The simple linear model including no effect of sex or start time of nesting was thus kept for the rest of analyses, and indicated a weak trend of decreasing duration of foraging trips through time since hatching (-2.629 ± 1.388, $t(27) = -1.893$, $p = 0.060$; Table 5; Fig. 1B).

Effect of frequency of foraging trips on reproductive success

We divided the post-hatching phase into three stages: early pre-flight (weeks 1–4 post-hatching), late pre-flight (weeks 5–8) and post-flight (weeks 9–12; Clark 1980). The frequency of foraging trips increased at each stage of chick development. However, the effect of the frequency of foraging trips on reproductive success was not significant during the early pre-flight stage (weeks 1–4; $Z = 1.025$; $p = 0.306$; Table 6). Frequency of foraging trips during the late pre-flight stage had a significant positive effect on reproductive success ($Z = 2.929$; $p = 0.003$; Table 6; Fig. 2). Note that the mean frequency of foraging trips during the early pre-flight stage and during the late pre-flight stage were not correlated ($r = 0.216$, $t(27) = 1.148$, $p = 0.261$).

Nest attendance and risk of takeover

Both adults from each pair were simultaneously present at the nest for more than half of the time during nest building and the first week of nest incubation; however, this proportion rapidly decreased during incubation. Until the beginning of the early pre-flight stage, there was at least one adult constantly at the nest. Then, the presence of even one adult gradually decreased, until a minimum of about 10 % of the time at the end of the nesting season (Fig. 3A). Most of the takeovers happened between February 13 to March 19 2017 (Fig. 3B). However, we found that the amount of time with presence of at least one parent at the nest did not significantly affect risk of successful takeovers ($e^{\beta} = 1.030$, $Z = 1.289$; $p = 0.197$; 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 initiation of incubation had a large positive effect on the risk of takeovers, with later initiation dates being associated to higher risk ($e^{\beta} = 2.135$; $Z = 1.971$; $p = 0.048$; Table 7; Fig. 3C).

Discussion

In agreement with our predictions, we found that the mean frequency of foraging trips per hour showed a gradual increase in time with developmental stage of chicks. However, our sample of chicks in the post-flight stage were small and highly variable among different pairs, thus limiting our inference during the final stage. The duration of foraging trips was not influenced by the developmental stage of chicks. These results are in general agreement with the literature on Wood Storks (Clark 1980, Bryan *et al.* 1995, 2005). Parents meet the increased energetic needs of chicks (Kahl 1962) by increasing the number rather than the length of trips (Bryan *et al.* 1995). During the post-hatching phase, the mean frequency of foraging trips per hour and their duration were not different between sexes, and were not related to the onset date of incubation. It is unclear whether duration of foraging trips is always stable as chicks grow, and it probably depends on the mosaic of wetland conditions in the area surrounding the colony (Coulter and Bryan 1993, Bryan *et al.* 1995).

We found that the mean rate of foraging trips in the late pre-flight stage, but not in the early pre-flight stage, affected the proportion of chicks that fledged. The highest chick survival ($p = 1$) corresponded to pairs exhibiting the highest mean frequency of foraging trips per hour (0.25 to 0.35 h^{-1}), while pairs obtaining the lowest chick survival ($p = 0.5$) had the lowest mean frequency of foraging trips per hour (0.12 to 0.16 h^{-1}). It is important to note the possible circularity of this relationship: in fact, one could 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, rather than the other way around. However, our results showed that the relationship between reproductive success and frequency of foraging trips is independent of the absolute number of fledglings. For instance, pairs with two successful chicks but low fledging success 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 success ratio of 0.5, see Fig. 2) foraging trip frequency than those with 100 % success ratio (0.17–0.23 h-1, see Fig. 2). If the absolute number of chicks was driving the frequency of foraging trips, we would expect the same frequency for an equal number of chicks independently from the initial brood size. This result supports an effect of foraging trip frequency in determining chick survival ratio, and not vice-versa. Since we did not find an effect of the frequency of foraging trips on the absolute number of fledglings ($Z = 1.035$; $p = 0.438$), our results suggest that other factors primarily determine it, such as mortality related to predation, sibling competition, or disturbance, as well as factors affecting clutch size in the first place (Burger 1982, Rodgers 1987, Bouton *et al.* 2005).

Takeover behavior appears to be widespread in Wood Storks, where it may affect more than a third of pairs in a colony (Bryan and Coulter 1991). In our study, (33 %) of nests experienced a takeover. The risk of undergoing a takeover was more than double for late pairs (nest initiation after February 13th). 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). Our results also indicated that the time of simultaneous nest attendance by both parents did not reduce the occurrence of takeovers. On the contrary, and surprisingly, pairs with greater nest attendance times by both individuals had a higher chance of undergoing a takeover. Since Bryan and Coulter (1991) found that all takeovers occurred when a single individual was present in the nest, we expected that pairs that spent more time together at the nest would have a lower chance of getting their nest taken over, but instead, we found that the presence of both individuals was associated with a higher risk of undergoing a takeover. It is possible that pairs increase joint attendance when their perceived risk of attack is greater, but we have no data with which to test this possible explanation. In any case, increased parental attendance did not result in reduced risk of nest failure, suggesting that there may sometimes not be a clear trade-off between attendance and time spent foraging. Similarly, the risk of reproductive failure due to nest takeover was higher for late nesters.

Wood Storks have long breeding cycles (~110 days), and are often limited by food availability at the end of the dry season. Our results demonstrate that the frequency of foraging trips during the late pre-flight stage is positively associated with reproductive success in Wood Storks. To our knowledge, this is the first time a link is established between parental effort and reproductive success for this species. Moreover, our findings highlighted an important mechanism of nest failure, nest takeovers, and that the risk associated with it varies throughout the season. Thus, in addition to constraints related to seasonal water level fluctuations, a late nesting initiation can be associated to low reproductive success due to a higher probability of takeover events.

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Supplemental Material

Appendix 1: 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.

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

Tables

Table 1. Reproductive success outcome: 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).

Table 1.

# 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

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.

Table 2.

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.

Table 3.

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

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.

Table 4.

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.

Table 5.

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

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

Table 6.

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

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^{β} = 2.135).

Table 7.

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

Figure captions

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).

Figure 2. Reproductive success ratio as a function of frequency of foraging trips in late pre-flight stage. 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).

Figure 3. Nest attendance of adult Wood Stork through time (A). 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. Kaplan-Meier survival curve (with confidence interval) for the risk of nest takeovers in 79 Wood Stork nests as a function of (B) the week of the year, or (C) week since start of incubation. Colors further distinguish between early pairs (red), and late pairs (blue).

Figures

Figure 1.

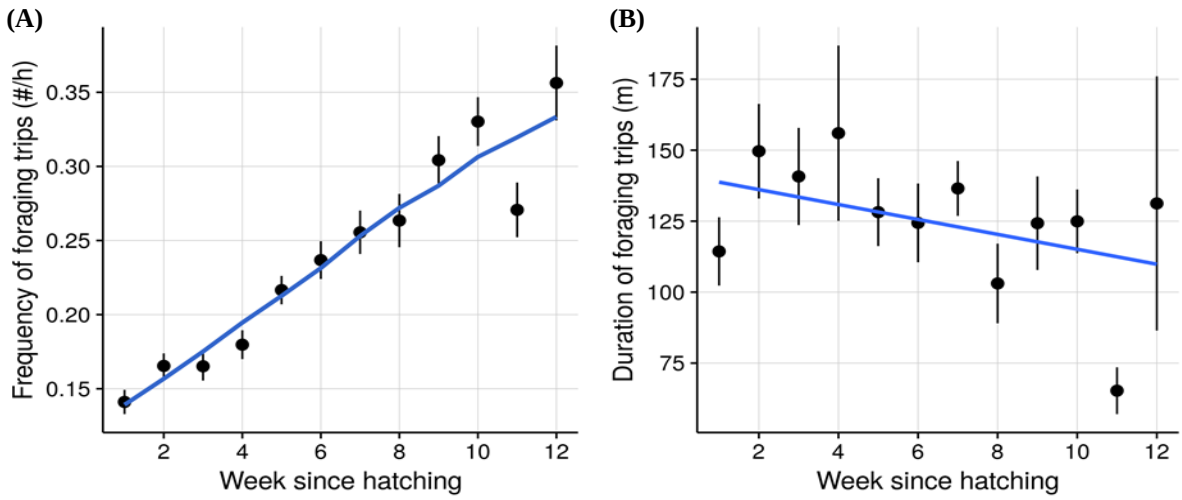
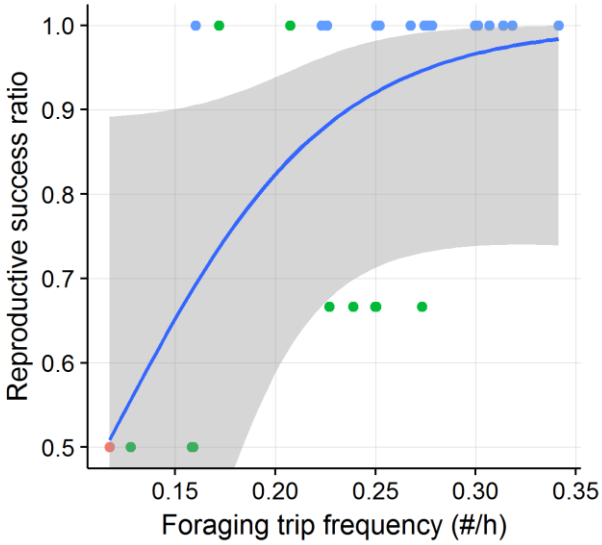
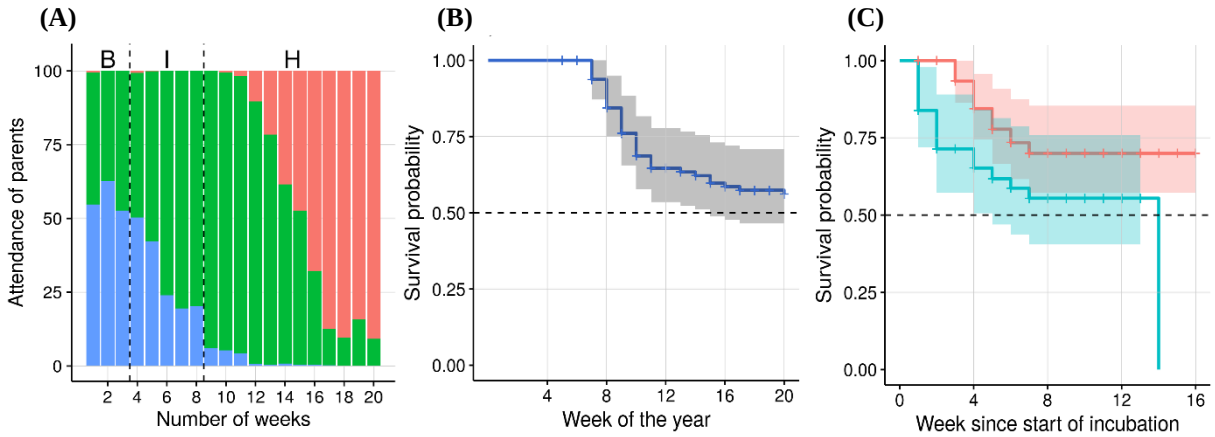


Figure 2.


Reproductive success ratio
1.0
0.9
0.8
0.7
0.6
0.5
0.15
0.20
0.25
0.30
0.35
Foraging trip frequency (#/h)

1032

Figure 3.



Photography

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

Plate 1.