Effects of Tourist Disturbance on Wood Stork Nesting Success and Breeding Behavior in the Brazilian Pantanal

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Abstract.—Large colonies of nesting ciconiiform birds have recently become an important tourist attraction in the Brazilian Pantanal. Visits to these colonies are uncontrolled and there is growing concern about disturbance to the breeding birds. In 1998, an experiment was conducted using different treatments within a single, large, heavily visited colony to assess the effects of different kinds of tourist viewing on the breeding behavior and nesting success of the Wood Stork (*Mycteria americana*). Pedestrian viewing, when more than 75 m from the nearest active nest, produced no detectable change in breeding success or behavior. However, boats passing within 20 m of nests were associated with significant changes in the time budgets of incubating adult storks. Most breeding failure occurred prior to hatching and was significantly higher in the boat-treatments in comparison with controls. It is suggested that the elevated level of nest failure observed in the boat-treatment group is evidence of biologically significant disturbance. These conclusions are supported by observations taken in 2000 when boats were excluded from the colony. Behavioral responses at the time of disturbance are typically used as indicators of effects when determining safe approach distances for birds. However, in this study, behavior during disturbances was unrelated to the eventual effect of disturbance. These findings have been incorporated into suggestions for the measurement of disturbance and management of tourist visits to bird colonies. *Received 11 May 2005, accepted 12 September 2005.*

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The rapid growth of ecotourism worldwide is putting increasing pressure on wildlife in areas that have historically been isolated and/or protected (Giannecchini 1993). In the Brazilian Pantanal, large breeding colonies of long-legged wading birds (200-10,000 pairs) have become an important attraction in a growing ecotourism industry. While this is a significant source of revenue for local communities (Bouton and Frederick 2003), there is growing concern that visits to the colonies are unregulated and often unguided. It has been suggested that the failure of particular breeding colonies is directly attributable to the activities of tourists in and around the colonies (Yamasita and Valle 2003). There is therefore a need for a reliable management protocol. Our study was designed to examine the possible effects of tourist disturbance on colonially nesting birds in a heavily visited colony, and to produce better-informed management of tourist visits.

Most studies of human disturbance in birds assume that an effect of disturbance will be demonstrated in overt stress behavior, such as flushing and mobbing at the time of disturbance (Burger 1981; Yalden and Yalden 1990). While behavior may indicate biologically meaningful stress, it is not clear that the absence of an overt reaction indicates a lack of disturbance. For example, penguins exposed to tourist visits exhibit no behavioral response to human presence, but show increased heart rates (Wilson *et al.* 1991), increased stomach temperature (Regel and Pütz 1997), avoidance behavior (Wilson *et al.* 1991) and changes in nest attendance behavior (Davis 1982). Nonetheless, stress behavior continues to form the basis of most recommended setback distances and management suggestions (Kury and Gochfeld 1975; Rodgers and Smith 1995; Rodgers and Schwikert 2002, 2003).

Colonially nesting birds are particularly vulnerable to human disturbance because large numbers of individuals and nests may be affected during any one event (Rodgers and Burger 1981; Burger 1981; Götmark 1992). Documented behavioral responses of these birds to human disturbance include nest desertion (Burger 1981; Safina and Burger 1983), reduced recruitment of new nesters (Tremblay and Ellison 1979), increased predation (Ellison and Cleary 1978) and colony abandonment (González 1997). Responses may also include modified chick and adult behavior (Rodgers and Burger 1981; Parsons and Burger 1982; Wilson *et al.* 1991), including changes in the severity of alarm and flushing responses (Burger 1981; Yalden and Yalden 1990). These may in turn result in changes in incubation time and energy expenditure (Cairns 1980; Safina and Burger 1983; Yalden and Yalden 1990; Yalden 1992). Responses to human disturbance vary with stage of nesting and type of disturbance (Frederick and Collopy 1989a; Erwin 1989) as well as habitat, food supply and species (Erwin 1989; Rodgers and Smith 1995).

It is important to note that not all of these effects may be biologically meaningful in measuring detrimental effects of human disturbance. For example, if a bird temporarily flushes from its nest, but does not suffer decreased reproductive success as a result, then the disturbance can be argued not to have had a real effect. Nisbet (2000) argues that only reductions in breeding success, increased adult mortality or declines in local, regional or total numbers can be considered adverse effects because birds are unlikely to be able to compensate for these losses.

In light of the studies discussed above, a test for responses to disturbance that would be evident in addition to, or even in the absence of, overt alarm responses seemed necessary. The hypothesis tested in this study was that a response to disturbance would be manifested in decreased reproductive success and subtle changes in the nesting behavior of adult birds. A field experiment was conducted at a single large colony using various types of existing tourist disturbance to test for effects on nesting success and breeding behavior of the Wood Stork (*Mycteria americana*).

METHODS AND STUDY AREA

The Brazilian Pantanal is a large, seasonally flooded, freshwater wetland in which breeding colonies of Ciconiiform birds are common. The Porto da Fazenda wading bird colony is located on the bank of the Cuiabá River (16°28.21'S, 056°07.567'W) between Barão de Melgaço and Porto Cercado, and can only be reached by boat. In both 1997 and 1998, the maximum size of the Porto da Fazenda colony was 600-700 nesting pairs, spread unevenly over approximately 1 km^2. The colony was composed principally of the Wood Stork (*Mycteria americana*) but also included Roseate Spoonbill (*Ajaia ajaja*) and, in 1997, Great Egret (*Ardea alba*). The colony forms annually during the dry season (June-November) in riparian forest bounded on two sides by the Cuiabá River and an oxbow cut-through (Rio Urutubinha) and, on the other two sides, by pastureland actively used for cattle grazing. For the last ten years this colony has been subject to increasing numbers of unregulated tourist visits, including boat and walking tours (Bouton 1999).

During 1998, in collaboration with a local environmental organization, Associação Ecológica Melgassense (AMEC), a management plan was developed for the colony. This allowed an opportunity to manipulate tourist activities and to monitor the effects of those manipulations. Tourists viewed the colony by boat or by visiting a walking trail with a trained guide (for details see Bouton 1999).

Experimental Groups

Three experimental groups of nests that were each exposed to a different disturbance treatment were monitored: control, boat traffic, and pedestrian tourist traffic. It was assumed that the distance between groups (>200 m) was enough to ensure exposure to specific, non-overlapping types of disturbance. In testing for the effects of disturbance it was assumed that adult birds in different groups were representative of a similar range of ages and similar exposure to disturbance, and that all treatments within the colony were equally exposed to external factors such as fluctuations in local prey availability and inclement weather.

1) *Boat-treatment* (N = 53 nests). A small river, Rio Urutubinha, bounds one side of the colony and is used by tour guides and boat drivers to show the nests at close range. Nests were in branches over hanging the river and in most cases boats passed within 20 m of nests. Observations of this treatment group began on 2 July 1998, from a blind placed behind vegetation on the far bank of the river (approx. 30 m distant).
2) *Pedestrians-treatment* (N = 17 nests). Starting 24 June 1998, a group of nests was monitored from a blind 80 m from the birds, on a walking trail that brought tourists to within 75 m of the nests. Pedestrians were visible to all of these birds.

3) *Control treatment* (N = 26 nests). These nests were never approached closer than 200 m by boats or pedestrians, although boats passing on the river were visible to the birds. Observation of this experimental group began on 3 July from the opposite side of the Cuiabá River (approximately 200 m distant).

Blinds were entered from the same access trails that tourists used, and observations began 15 minutes after arrival of the observers to allow birds to resume normal activity. Observation time and number of observation days for each treatment are given in Table 2.

Nests at all sites were densely packed (approx. 2 m between nearest neighbors) and were in trees over 10 m above the ground. The majority of nests were located in Cabaceira (*Crataeva tapia*) or Biguazeiro trees (*Albizia polyantha*), often making use of natural platforms of climbing vines, including Cipó-de-leite (*Ipomoea rubens*; Pott and Pott 1994).

Behavioral Observations

All nests were monitored from the initiation of nest building (early July) to the time when the first cohort of chicks fledged (end of September). Observations were made at each site every 2-3 d from 07.00 h to 11.00 h. The behavior of adults at each nest was categorized during instantaneous scan samples once every five minutes (Altmann 1974; Lehner 1996). Behavior categories were defined based on Kahl (1972) and on our previous observations of the Wood Stork (Table 1). The sequence of sampling individual nests was the same for all observations. The largest experimental group, the boat traffic site, was divided into two groups for observation to ensure that observers never scanned more than 30 nests at a time. When 30 nests were scanned, sampling took approximately 70% of the 5-minute inter-scan interval.

Any newly deserted nests or newly hatched chicks were noted. The reaction of adult Wood Storks to passing boats or pedestrian tours was recorded using the following scale: (1) no visible reaction, (2) birds stand up, (3) birds flap wings, (4) some birds take flight and (5) all birds take flight. These levels of response were based on behavioral sequences observed in the field as nesting birds were approached during experimental visits in 1997.

Additional Observations in 2000

In 2000, AMEC, the non-profit organization responsible for managing tourist activities at the colony, chose to modify the management strategies based on findings of the 1998 study. The river that passed under nests (Rio Urutubinha) was closed to boat traffic and a 500m walking trail was established on the far side of that river so that tourists could view birds on foot. All tourists received instruction on how to minimize the impact of their presence and visited the trail with local guides trained by AMEC. The results of these efforts were monitored using nest abandonment, total success, fledging success and chick survival in a control area of the colony (N = 94 nests) compared with the nests in the area previously exposed to boat-disturbance (N = 137 nests). Nests were mapped in the last week of June and observed every 3-4 days throughout the nesting season.

Statistical Analysis

To account for changes in adult behavior as the nesting season progressed, the stage of nesting was categorized into four nesting intervals: (1) courtship and nest construction, (2) incubation, (3) young chicks (≤21 days of age) and (4) older chicks (>21 days of age). Egg-laying dates were estimated from observed hatching dates using an incubation period of 30 d (Palmer 1962).

Table 1. Behavioral criteria used to define the behavior of adult Wood Storks during scan samples. Behavior patterns marked with an asterisk (*) are as defined by Kahl (1972).

Behavior	Criteria
Sitting	Adult sitting on nest.
Flying	Flying into or leaving nest with or without green twigs or sticks.
Standing-over	Standing on nest or just outside of it. This category includes behavior such as wing-flaps, up-down movements of the head* and interactions with con-specifics on neighboring nests e.g. snap displays.*
Spread-wing*	Standing over nest with wings spread in a loose "D" shape, usually leaning forward over nest. We believe this behavior was most often adopted in order to shade nest contents.
Nest maintenance	Adult standing over nest with head down, often throwing out old fish, moving twigs and leaves or swaying-twig-grasping*, which involves working a twig into the nests by gently moving it from side to side so that the bird is swaying. Also includes gathering nest material which involves the attending adult standing and reaching to pull twigs and leaves from surrounding nests or trees.
Preening*	Adult cleaning its feathers. This category also includes rousing* in which wings are held away from body and shaken, followed by short head-shakes; head rub* in which the head is thrown back so that crown rests on the upper back and is rotated from side to side; and wing and/or leg stretches.
Pair interactions	Primarily sexual displays but includes: allo-preening (members of a pair preen one another), Copulation and Up Down Simultaneous* when both members of the pair move their heads up and down together.
Interactions w/ chicks	Adult feeding chick or bringing water to it. Also, includes adult preening the chicks usually around the head and neck.

Any observations made before that date were considered to be during courtship and construction. If a nest was deserted before hatched young were observed, a laying date of 9 July was assumed, which was the modal time at which eggs in all nests studied were laid.

The behavior of individuals at nests within a treatment was assumed to be independent. The proportion of time spent in each of the nine behavior categories was used to create a time budget for each nest on each observation day. An arcsine square root transformation was applied to these proportions to improve normality and variance (Zar 1984). We tested for differences in transformed proportions of each activity between disturbance treatments with an analysis of variance (ANOVA; Zar 1984) using nest number within site as an error term (covariance structure was compound symmetry). To account for the lack of independence due to multiple observations of the same nest, errors associated with the same nest were allowed to be correlated. No covariates were used in the ANOVA. In this way, the ANOVA functioned as a screening tool to determine which behavior categories showed a significant effect of treatment. If a significant difference was detected for a specific activity, we performed post-hoc Bonferroni comparisons using multiple pair-wise t-tests, applied to least squared means of the transformed proportions, to determine which of the three treatments differed significantly from the control. Differences between treatment groups in percentage of time adults were present at the nest were tested in the same way.

Several measures of nesting success were compared including: number of nest desertions; total success (number of chicks fledged per nest start); fledging success (number of chicks fledged per successful nest); chick survival; and hatch success in control and treatment groups using 2-by-2 Chi-square tests and non-parametric Wilcoxon tests. All analyses were performed in SPSS 12.0 for Windows.

RESULTS

Levels of Disturbance

Visitation of tourists to the Porto da Fazenda colony changed significantly as the nesting season progressed (Mean = 5.6, 3.3, 1.9 boats/d for July, August and September, respectively). Most boats passing under boat-treatment nests were carrying tourists in all three months of this study (58% of total, range among months 50-63%). Sport fishermen accounted for 20% of the total (range 15-25%) and the remainder of boat-trips was forestry police and local inhabitants.

Based on results from questionnaires distributed to tourists (see Bouton 1999 and Bouton and Frederick 2003) an estimated 3% of tourists used only the walking trail, 38% of tourists saw the colony only by boat and 59% used both methods to view the colony. Thus the two treatments (walking and boat) represent different frequencies of disturbance as well as different kinds of disturbance.

Behavioral Observations

Approximately 94 h of behavioral scans were collected at the boat-treatment group, 106 h at the pedestrian-treatment nests, and 103 h at control nests.

Boats were observed passing under nests in the boat-disturbed group on 89 occasions. During 81% of these visits the storks exhibited no behavioral reaction to the disturbance. Only 6% of the visits caused sitting birds to stand up, 5% caused some birds to flap their wings, and 9% caused some birds to flush. Generally, only one member of each pair flushed, so nests were rarely left unattended. On no occasion were all of the birds under observation flushed from their nests at once. Birds observed during walking tours never showed behavioral responses to the disturbance.

During nest construction and courtship, pedestrian-treatment birds spent more than twice as much time in nest maintenance and standing over the nest than did the controls, and significantly less time sitting on the nest (see Table 2). During incubation the boat-treatment birds spent 20% less time sitting on nests, and more time in nest maintenance, preening, standing over the nest and in spread-wing posture than controls (Table 2). Exposure to sun was not controlled in these analyses, but there were no significant differences in mean temperatures during observation between control and boat-treatments (control: average 25.9 ± 3.5°C; boat treatment: average 26.5 ± 3.3°C).

In the post-hatching stage, there were no differences in time budgets of storks in different treatment groups. During the small chick stage, the only significant difference was that boat- treatment birds were observed in the spread-wing posture significantly more often than were control birds (Table 2).

In the large chick stage, boat-treatment adults spent significantly more time interacting with their chicks, and specifically in preening chicks, than did controls (Tables 2

Table 2. Mean untransformed percentages (± 1 SE) of time adult Wood Storks spent in different activities by treatment and nest stage at Porto da Fazenda, 1998. Bold nest stages showed a significant effect of treatment on transformed proportions of time spent in that activity (2-way ANOVAs). Treatments that differed significantly from the control (post-hoc Bonferroni comparisons) are marked: *P < 0.05, **P < 0.01, ***P < 0.001. Number of nests and days of observation per nesting stage per treatment are given in italics at the top of the table.

		Disturbance treatment		
Activity	Nesting stage	Control	Boats	Pedestrians
Nests observed	Construction	20 (8)	46 (11)	13 (9)
(Days observed)	Incubation	26 (16)	53 (20)	17 (17)
	Small chicks	18 (12)	18 (14)	16 (12)
	Large chicks	13 (12)	7 (9)	12 (12)
Nest maintenance	Construction[1]	15.6 ± 1.7	15.1 ± 0.9	21.3 ± 1.7*
$F^1_{2,47} = 4.1, P < 0.05$	Incubation[2]	11.0 ± 0.7	15.6 ± 0.6***	10.5 ± 0.8
$F^2_{2,92} = 19.8, P < 0.001$	Small chicks	14.5 ± 1.4	15.0 ± 2.0	13.9 ± 1.5
	Large chicks	4.3 ± 0.8	7.8 ± 1.2	7.0 ± 0.9
Flying	Construction	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Incubation	0.0 ± 0.0	1.0 ± 1.0	0.0 ± 0.0
	Small chicks	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.0
	Large chicks	0.7 ± 0.1	0.3 ± 0.12	0.6 ± 0.2
No adult	Construction	1.0 ± 0.8	1.6 ± 0.7	0.1 ± 0.1
	Incubation	1.1 ± 0.8	2.5 ± 0.7	0.0 ± 0.0
	Small chicks	3.4 ± 1.8	2.4 ± 1.4	2.2 ± 1.6
	Large chicks	34.4 ± 6.2	13.0 ± 6.7	20.0 ± 5.7
Pair interactions	Construction	1.0 ± 0.2	1.3 ± 0.2	2.0 ± 0.4
	Incubation	0.3 ± 0.1	0.7 ± 0.1	0.2 ± 0.1
	Small chicks	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.1
	Large chicks	0.2 ± 0.1	0.2 ± 0.2	0.3 ± 0.1
Interactions w/ chicks	Small chicks	2.4 ± 0.4	3.2 ± 0.3	2.1 ± 0.4
$F^1_{2,20} = 6.7, P < 0.01$	Large chicks[1]	2.6 ± 0.5	8.0 ± 2.5**	1.9 ± 0.2
Preening	Construction	7.7 ± 1.4	9.7 ± 1.4	14.8 ± 1.5
$F^2_{2,92} = 10.3, P < 0.001$	Incubation[1]	5.0 ± 0.7	8.9 ± 0.7***	6.5 ± 0.8
	Small chicks	17.7 ± 1.7	22.6 ± 4.3	22.0 ± 1.5
	Large chicks	12.5 ± 1.3	15.3 ± 2.7	14.6 ± 1.4
Sitting	Construction[1]	64.9 ± 5.2	54.4 ± 3.9	33.8 ± 4.6**
$F^1_{2,62} = 5.8, P < 0.01$	Incubation[2]	77.9 ± 2.7	58.2 ± 2.7***	78.8 ± 1.86
$F^2_{2,90} = 19.6, P < 0.001$	Small chicks	21.2 ± 5.4	26.6 ± 8.5	24.1 ± 3.2
	Large chicks	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Standing over	Construction[1]	9.9 ± 2.3	17.8 ± 2.2	28.0 ± 3.2
$F^1_{2,55} = 3.3, P < 0.05$	Incubation[2]	3.4 ± 1.0	10.9 ± 1.3**	2.8 ± 0.6
$F^2_{2,111} = 13.6, P < 0.001$	Small chicks	31.4 ± 4.3	36.2 ± 5.8	27.7 ± 2.7
	Large chicks	42.1 ± 4.4	48.0 ± 4.6	50.0 ± 4.9
Spread wing	Construction	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
$F^1_{2,85} = 6.2, P < 0.01$	Incubation[1]	1.0 ± 0.3	2.4 ± 0.4*	1.1 ± 0.3
$F^2_{2,37} = 3.4, P < 0.05$	Small chicks[2]	9.3 ± 1.7	12.9 ± 2.3	7.9 ± 1.3
	Large chicks	3.3 ± 1.3	7.5 ± 2.7	5.7 ± 1.8

and 3). There were no significant differences between treatments in proportion of time spent feeding or watering of chicks in either nesting stage. Adults in the boat-treatment did not spend significantly more or less time at the nest during the large chick stage than did controls.

Adult Attendance

The percentage of time that at least one adult was present at the nest decreased markedly in all treatment groups after the large chick stage (Table 4). From initiation of nest building to the time when the chicks were

Table 3. Percentage of time (± 1 SE) that adult Wood Storks spent in different activities categorized as "interactions with chicks" by treatment and nest stage at Porto da Fazenda, 1998. The time spent preening large chicks differed significantly between experimental treatments (2-way ANOVA, $F_{2,15} = 4.4$, $P < 0.05$, marked with an asterisk (*)), and post-hoc Bonferroni comparisons revealed that adults in the boat-treatment spent significantly more time preening large chicks than did controls ($P < 0.05$, marked with two asterisks (**)). Sample sizes are given in Table 2.

		Disturbance treatments		
Activity	Nesting stage	Control	Boats	Pedestrians
Preening chicks	Small chicks	0.4 ± 0.2	0.8 ± 0.3	0.3 ± 0.1
	Large chicks*	1.0 ± 0.5	6.4 ± 2.8**	0.5 ± 0.1
Feeding chicks	Small chicks	1.9 ± 0.3	1.9 ± 0.2	1.8 ± 0.3
	Large chicks	1.5 ± 0.2	1.5 ± 0.5	1.3 ± 0.2
Watering chicks	Small chicks	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
	Large chicks	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1

approximately three weeks of age, at least one adult was at the nest for more than 95% of the time, with no significant differences between treatments.

The percentage of time that both adults were present simultaneously at the nest also declined during the nesting cycle (Table 4). During the incubation period, both adults attended simultaneously at the boat-treatment nests significantly more often than at control nests.

Nest Desertions

Nest failure varied dramatically between treatment groups (Table 5). Analyses of these data excluded nests lost during a single very violent thunderstorm in which chicks or entire nests were knocked out of trees, and when the nest loss seemed to exclude abandonment decisions by the adult. Overall, the boat-treatment group differed significantly from the control in the proportion of nests deserted ($\chi^2_1 = 18.1$, $P < 0.001$).

The timing of nest desertions was relatively synchronous among the four treatments. The daily abandonment rate increased steadily from a few nests per day in July, to a peak in the middle of August followed by a rapid decline. At the time of abandonment the vast majority of nests contained eggs (eggs = 72%, chicks aged 0-7 d = 6%, 8-14 d = 10%, 15-21 d = 4%, 22-28 d = 7%, 29+ d = 1% (N = 90 nests)).

The number of chicks fledged per nest started (total success) was significantly lower in the boat-treatment than in the control (Wilcoxon test: $Z = 4.36$, $P < 0.001$. Table 5), but there was no significant difference between the pedestrian and control treatments

Table 4. Mean percentage of time (± 1 SE) that adult Wood Storks spent at the nest, by nesting stage at Porto da Fazenda, 1998. The proportion of time that both adults were present simultaneously differed significantly between experimental treatments during incubation (2-way ANOVA, $F_{2,96} = 9.9$, $P < 0.001$. Shown with an asterisk (*)). Post-hoc Bonferroni comparisons revealed that adults in the boat-treatment spent significantly more time present together at the nest than did controls ($P < 0.001$, marked with two asterisks (**)). Sample sizes are given in Table 2.

		Disturbance treatments		
Adult presence	Nesting stage	Control	Boats	Pedestrians
At least one adult present at nest	Courtship	99.0 ± 1.2	98.2 ± 0.8	100 ± 1.3
	Incubation	99.0 ± 0.9	97.4 ± 0.6	100 ± 1.0
	Small chicks	96.7 ± 1.4	98.7 ± 1.6	97.8 ± 1.3
	Large chicks	65.4 ± 6.1	87.4 ± 13.5	80.6 ± 6.5
Both adults present at the nest simultaneously	Courtship	47.7 ± 4.3	53.0 ± 2.9	55.9 ± 4.7
	Incubation*	20.7 ± 2.9	34.5 ± 2.5**	18.5 ± 3.1
	Small chicks	1.9 ± 0.9	1.2 ± 1.1	1.9 ± 0.9
	Large chicks	0.5 ± 0.2	0.3 ± 0.5	0.8 ± 0.2

Table 5. Nesting success measures: percentage deserted; fledging success (number of chicks fledged per successful nest); total success (number of chicks fledged per nest start); hatch success (maximum number of chicks observed per nest that hatched chicks); and chick survival, for Wood Storks at Porto da Fazenda colony in 1998. The boat-treatment but not the pedestrian-treatment differed significantly from the control group in all measures of nest success (marked with an asterisk (*): Chi-squared for percentages and Wilcoxon for total and fledging success, $\alpha = 0.05$). N^1 is number of nest starts, and N^2 is the number of nests that hatched at least one chick.

Treatments	N^1	% deserted	Fledging success	Total success	N^2	Hatch success	% chick survival
Control	27	56	2.0	0.9	19	2.1	62
Boats	47	96*	1.0*	0.1*	16	1.4*	13*
Pedestrians	14	36	1.9	1.2	14	2.1	63

($Z = 0.98$, n.s.). The number of chicks fledged per successful nest (nests that raised at least one chick to fledging) was highest in the control group and significantly lower in the boat-treatment group ($Z = 2.05$, $P < 0.05$) but not in the pedestrian-treatment ($Z = 0.48$, n.s., Table 5).

Hatching success was estimated using the maximum number of chicks observed at any one time within a treatment, divided by the number of nests in the treatment that hatched chicks (Table 5). Hatching success was highest in the control group and significantly lower in the boat-treatment group ($Z = 2.58$, $P < 0.02$) but not in the pedestrian-treatment ($Z = 0.04$, n.s., Table 5). Chick survival (chicks fledging divided by chicks hatching, not including chicks lost during storms) was significantly lower in the boat-treatment than in the control ($\chi^2_1 = 10.0$, $P < 0.001$, Table 5).

Results of Boat Exclusion

During the exclusion of boats from the colony in 2000, the same four reproductive parameters were monitored as in 1998: percentage nest failure; total nest success; fledging success; and chick survival at the same two sites as in 1998. Despite the strong differences among sites in 1998, there were no significant differences in the same parameters in 2000 (Table 6); both 2000 groups showing breeding success similar to that of the control group in 1998 (Table 5).

DISCUSSION

Effects of Human Disturbance on Nest Success

Despite only minor changes in time budgets, the boat-disturbance group showed dramatically decreased nest success (total success, fledging success, hatching success and chick survival) when compared with both the pedestrian-treatment and control groups. Conversely, when boats were excluded from the colony in 2000, nesting success in the same area did not differ significantly from that of control nests. The latter data lend strong support to the suggestion that the decline in nesting success seen in 1998 was due to boat disturbance and not some other unmeasured variable. Boat disturbances at Porto da Fazenda negatively affected Wood Stork reproduction.

It is possible that boat-treatments may have affected the behavior of the chicks directly, which might explain some of the decrease in chick survival that we observed.

Table 6. Desertion rate, total success (number of chicks fledged per nest start), fledging success (number of chicks fledged per successful nest), and survival of Wood Stork chicks at Porto da Fazenda colony in 2000. The disturbance treatment did not differ significantly from the control in any of these measures (Chi-squared for percentages and Wilcoxon for total and fledging success, $\alpha = 0.05$). N is number of nests.

Treatment	N	Total success	% Desertion	% chick survival	Fledging success
Control group	94	0.7	54	58	1.5
Boats removed	137	0.7	51	58	1.4

Human disturbance has been associated with reduced body mass and slower growth of cormorant and puffin chicks (Kury and Gotchfeld 1975; Pierce and Simons 1986), as well as with changes in chick behavior (night herons, Parsons and Burger 1982). Penguin chicks show more physiological stress at low levels of disturbance than adults (Regel and Pütz 1997), indicating that chicks may be particularly sensitive to disturbance. Our study did not address changes in chick behavior, but this may be an important factor in determining how disturbance affects post hatching survival.

In contrast to the boat-treatment group, the 1998 nesting success in the pedestrian-treatment did not differ significantly from that in the control group. These results suggest that pedestrian viewing from 75 m did not significantly affect nesting success. This conclusion is also supported by observations in 2000, in which tourists viewed nests from a trail on the far side of the river and not from boats, but they did not appear to cause any decrease in nest success in comparison with the control group.

The frequency of disturbance differed between treatments in 1998. Previous studies have shown that increased frequency of visitation may lead to differential exposure to thermal stress and predators when adults flush (Safina and Burger 1983; Piatt *et al.* 1990, but see Frederick and Collopy 1989a). However, since adult Wood Storks were never observed flushing from their nests in response to boats and walking tours, these mechanisms probably do not explain our treatment differences in breeding success. While different frequencies of disturbance may account for some of the differences in reproductive success, we believe that this effect is minimal.

Large-scale abandonment, sometimes of entire colonies, has been described in this species in other locations (Clark 1978; Ogden *et al.* 1987; Frederick and Collopy 1989b; Ramo and Busto 1992; Rodgers and Schwikert 1997; González 1999), often in response to unseasonable rainfall or human disturbance. In 1998, the Pantanal experienced a particularly dry "wet" season, and more rain during the dry nesting season than is normal. The number of young per nest (2.0, range 1-3) and the total success rate (0.89) of the control nests were at the low end of the range reported for breeding Wood Storks in Florida (Rodgers and Schweikert 1997). They were, however, comparable with measurements at colonies stressed by human disturbance in Venezuela (González 1999: fledging per nest = 1.67 and total success rate = 0.66). Consistent with the high abandonment levels observed at Porto da Fazenda, most colonies in the northern and southern Pantanal did not initiate nesting, or abandoned early in the breeding cycle (S. Nascimento, pers. comm.). Thus, it is likely that the high abandonment rates we recorded were a compounded result of external and disturbance stresses. This evidence of external stress is important, since under excellent breeding conditions the effects of human disturbance might have been less evident (see White and Thurow 1985). Further work is needed to determine whether human disturbance reduces resistance to other environmental stresses.

Behavioral Responses to Human Disturbance

Evidence from several studies suggests that some colonially nesting birds may habituate to human presence (Burger 1981; Rodgers and Smith 1995; Nisbet 2000), particularly if they are able to discern that humans present no threat (Burger and Gochfeld 1981). The idea that Wood Storks at Porto da Fazenda habituated is supported by observations of nests approached by pedestrians to within 20 m. Birds at these nests initially stood-up in response to the approach, but never flushed. By the third visit of this type, the birds exhibited no behavioral response (these nests were not included in any experimental group).

This habituation and the lack of behavioral responses in all groups at the time of disturbance are contrary to the significant relationship between nest failure and disturbance we observed. Thus, in our study, a bird's behavior during a disturbance event was a poor indicator of the eventual effect of that disturbance. We suggest that, in the Wood Stork, the effects of disturbance cannot reliably be judged using observations of immediate behavioral responses.

This finding has important implications for interpretation of setback distances based on flush responses. For example, Rodgers and Smith (1995) recommended a setback distance of 63 m for motorboats approaching Wood Stork breeding colonies, and Rodgers and Schwikert (2003) recommended 118 m for boats approaching foraging Wood Storks. These distances seem counterintuitive because it would be expected that breeding birds would need more protection than foraging birds. The fact that nesting birds might be less likely to flush probably reflects the difference in cost of evasive behavior: nesting birds potentially loose chicks or eggs to predation, heat or cold stress, whereas foraging birds loose only their immediate feeding success. Thus, the fact that foraging birds flush at 113 m suggests that nesting birds may also be stressed by a boat approach at 113 m, but that the cost of flushing may prevent them from departing until the boat approached to 63 m.

During incubation, boat-treatment birds spent significantly less time sitting on eggs than did control birds. Decreased incubation attentiveness has been suggested as a cause of decreased hatching in disturbed birds (Cairns 1980). This is supported by the reduced hatching success observed in the boat-treatment group. However, it is important to note that most of the boat-treatment nests did not survive until the normal time of hatching, so that the average nest attentiveness for this treatment may not have been representative of birds incubating eggs to term.

Though other studies of nesting birds have found that disturbance increases chick neglect and decreases nest attendance (Burger 1981; White and Thurow 1985), we found no evidence of these effects. In fact, the boat-treatment birds showed significantly more interactions with chicks, reflected in more time spent shading and preening chicks, than did controls. These trends contradict the idea that tourist disturbance leads to post-hatching nest neglect in the Wood Stork. However, increased attendance may have resulted in a decrease in the parents' cumulative foraging hours, which might decrease the total quantity of food delivered to the chicks. Further work is needed to determine whether disturbed nests receive the same quantity of food as undisturbed nests.

Management Implications

This study represents the results found in a single colony in one year, and as such represents an un-replicated experiment. Further replications of this work are necessary to better test these findings. Nonetheless, in light of previous studies, the results are not unexpected, and our study derives considerable validity from the size of the colony, the distances between treatment groups and the positive, predicted results seen when boats were excluded in 2000.

Evidence was found of subtle changes in stork breeding behavior and dramatic decreases in nesting success as a result of boat disturbance close (<20 m) to nesting birds. We therefore suggest that boat viewing be minimized and that the largest currently recommended "set back" distance for Wood Storks, 118 m (Rodgers and Schwikert 2003), is used.

Pedestrian viewing from 75 m did not appear to have adverse effects on nesting success or breeding behavior of Wood Storks. Carefully managed walking tours seem to be a realistic viewing option for managers of tourism in Wood Stork colonies. We caution, however, that longer-term effects of disturbance were not examined in this study, and remain possible (e.g., reduced philopatry to disturbed colonies). Long-term studies are needed to fully explore these effects. We also note that, in this study, human disturbance occurred despite the training of both guides and tourists (Bouton and Frederick 2003).

Responses to human disturbance are dependent upon nesting stage, species, type of disturbance, habitat type, food supply and even location (Frederick and Collopy 1989a; Erwin 1995; Rodgers and Smith 1995). Studies of human disturbance should be conducted wherever human activities occur close to colonially nesting birds. Studying behavioral responses in order to monitor the effects of disturbance or to design management protocols is not recommended as a single tool, as this and other studies show that a lack of behavioral response at the time of the disturbance does not necessarily indicate a lack of stress (Wilson *et al.* 1991; Regel and Pütz 1997). Instead, we suggest that monitoring of reproduction and settlement patterns over a number of years is necessary to confirm that tourist activities do not have any long-term impacts on breeding birds.

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