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Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*)

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Abstract

Ecotourism helps to protect many habitats, but may also have negative impacts on wildlife. We investigated effects of ecotourists on reproductive success of hoatzins (*Opisthocomus hoazin*) and on hormonal status of their chicks in Amazonian rainforest lakes by comparing birds from undisturbed and from tourist-exposed nests. Hatching success was similar in both groups but chick survival was much lower at tourist-exposed nests than at undisturbed nests. This effect was due to an increased mortality of juveniles prior to fledging whereas small nestlings seemed largely unaffected. Juveniles, but not nestlings, living at tourist-exposed sites had a lower body mass and showed a stronger hormonal response to experimental stress compared to individuals at undisturbed sites. These data suggest that juvenile hoatzins were susceptible to tourist-induced stress which in turn may be responsible for the lower survival. In contrast, adult hoatzins that were incubating had apparently habituated to tourist presence because their flush distances at tourist-exposed nests were 50% lower than at undisturbed sites. Our findings demonstrate that individuals in different life stages show different susceptibilities to tourism. We suggest that even just watching animals during breeding can threaten their survival, but a proper scientific management of off-limit zones and area-specific guidelines for wildlife observation could reduce harmful effects.

Keywords: Hoatzin; *Opisthocomus hoazin*; Ecotourism; Wildlife observation; Stress hormones; Rainforest; Conservation

1. Introduction

Ecotourism is largely perceived to safeguard pristine areas and thereby to contribute to the conservation of the rich tropical biodiversity (Groom et al., 1991a; Munn, 1992; Ceballos-Lascuráin, 1996). Revenue from ecotourism operations may compensate local people for the abandonment of other non-sustainable uses (Munn, 1992; Wunder, 1996) and might allow a gentle development of regions where economic alternatives are rare. Because ecotourism is a rapidly growing industry (Giannecchini, 1993), there is an urgent need to assess its impacts and develop rapid ways to avoid potential negative consequences.

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Protected rainforests areas are the favoured destinations of many ecotourists in tropical countries. One of the main travel incentives is to experience free-ranging animals in a pristine landscape (Boo, 1990). Whereas effects of tourism on wildlife are well recognised in temperate countries (reviews in Boyle and Samson, 1985; Edington and Edington, 1986; Knight and Gutzwiller, 1995), very little is known whether visitors have any influence on rainforest animals. The rare empirical evidence available indicates that even low numbers of visitors can change activity patterns or expel rainforest animals from potential foraging or breeding sites (Groom, 1991b; Griffiths and van Schaik, 1993; Schenck and Staib, 1998; de la Torre et al., 2000). All of these effects can reduce reproductive success and therefore hamper conservation goals of protected areas. At the same time negative impacts on wildlife reduce both the ecotouristic as well as the economic value of the visited area.

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Here, we concentrate on the Cuyabeno Wildlife Reserve which has become the most important destination for ecotourists in Amazonian Ecuador. Tourism started in the 1980s and developed quickly and largely uncontrolled since 1992. Ecotourists regularly search for close encounters with wildlife and the high visibility of birds make them a major attraction. One target is the hoatzin (*Opisthocomus hoazin*) whose pheasant-like size and colourful plumage with a crest make it conspicuous. Because tourists like to witness on animal's family life nest sites and young birds are particularly attractive. Reports by tourist guides indicated that hoatzins bred in larger numbers prior to regular tourism than nowadays (Aurora Payaguaje, Galo Sevilla, pers. comm.). In the present paper, we examined the effects of ecotourists on reproductive success of hoatzins in the Cuyabeno Lakes by comparing birds at undisturbed nests in off-limit zones and at tourist-exposed nests. We also measured stress hormones in hoatzin chicks to evaluate the physiological effects of human disturbances. Although field endocrinology is acknowledged as a useful tool in conservation (Wingfield et al., 1995; Schoech and Lipar, 1998), only a few studies have used the hormonal status of vertebrates as an assessment of tourism impacts so far (Fowler, 1999; Romero and Wikelski, 2002).

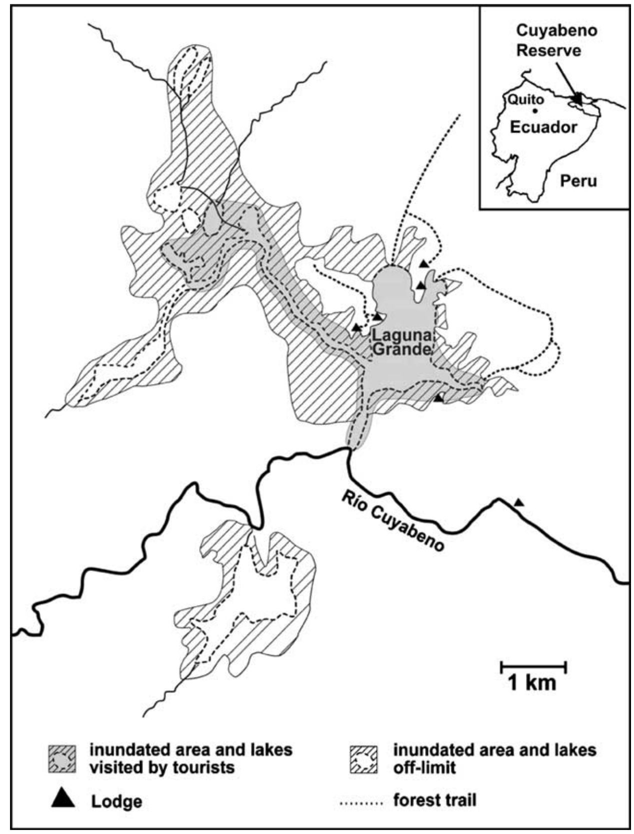

Fig. 1. The Cuyabeno Lakes in the Amazonian lowlands of Ecuador within the Cuyabeno Wildlife Reserve (0°02′N, 76°9′W and 0°03′S, 76°14′W). Modified after INEFAN-ONISE/OISE 1995.

2. Methods

2.1. Study site and tourism

The Cuyabeno Reserve is a protected rainforest area of about 6000 km^2, situated in the Amazonian lowlands of Ecuador. One of its main tourist sites are the Cuyabeno Lakes, a system of rivers and lakes with flooded and unflooded forests (Fig. 1). Providing an extraordinary landscape and rich wildlife, this rather small area (10×10 km) attracts ca. 4000 tourists per year. Tourists come all year round, but a pronounced high season exists in July and August when about 10 tourist groups with a total of more than 100 people may be based at the same time at the central Laguna Grande. Visitors go on guided jungle walks and explore the lakes and rivers by motorised and paddled canoes, normally of four days duration, to actively seek and approach animals. Most tourist sites are visited every day but boat traffic changes unpredictably: a day with only one boat could be followed by a day with six or ten boats in only two hours. Sites for tourism use and off-limit zones were established in 1996 for the area of the Cuyabeno Lakes (INEFAN-ONISE/OISE, 1995). However, using the argument that wildlife observation is quite harmless, several tour operators tried to suspend the ban on visiting some sites. For more details on the study area and tourism development, see Müllner and Pfrommer (2001).

2.2. Study species

The hoatzin (*O. hoazin*) is distributed patchily throughout the Amazon and Orinoco river basin and is locally common in the Cuyabeno Reserve. It inhabits the stretches of flooded forest which surround the Cuyabeno Lakes, living in pairs or small family groups and defending territories of about 5000–8000 m^2. Density of groups is 3–7 per km of shore line and lies within the range of another rainforest population of hoatzins in Peru (Torres, 1987). Breeding is closely linked to the beginning of the wet season and starts in April or May. Hoatzins build simple platform nests on branches overhanging the water, and 72% of nest sites in the Cuyabeno Lakes are situated on isolated flooded trees, which are well protected against non-flying and non-swimming predators. The modal clutch size is two eggs and the incubation period lasts 32 days; in 75% of broods only one chick survives until fledging (A.M., unpubl. data). If not disturbed, hatchlings stay in the nest 14–20 days and then begin to climb into the surrounding foliage. First flights occur at 7 weeks of age, and individuals reach full flight capabilities at about 10 weeks. As an adaptation to life in inundated forests, hoatzin chicks prior to fledging show an extraordinary escape behaviour when approached by a predator: they jump into the water and may dive 5–15 m in an attempt to escape. With the help of their wing claws they climb another tree, but do not return to their nest site. Instead, the adults normally find the young and feed them until fledging. The most common predators we observed in the Cuyabeno Lakes preying on eggs or young of the hoatzins were several species of toucans, raptors and snakes, while monkeys or other non-flying mammals were rarely seen. In contrast to reports from other regions (Beebe, 1909; Strahl, 1988) hoatzins in Cuyabeno neither defended the clutch nor their chicks, but always fled from a predator or an approaching observer.

Hoatzins feed only on foliage (Grajal et al., 1989) and were observed to feed on the most common trees and shrubs of their flooded habitat, mainly Leguminosae (A.M., unpubl. data). The chicks were fed a predigested mash that the adults regurgitated from their crops. Overall, food was sufficiently available during the entire breeding season. However, hoatzins prefer the young leaves and buds, whose main annual peak coincides with the feeding of the chicks in July and August.

2.3. Data collection and analyses

2.3.1. Monitoring of nest sites

The entire area of the Cuyabeno Lakes (ca. 50 km of shoreline) was checked regularly for hoatzin nests and breeding activities from April to October in 1996, 1997 and 1998. All data were collected by the same observer (A.M.) paddling a dugout canoe. Incubated nests were approached either only once, to inspect the nest content, or a second time to determine the flush distances of adults. To minimise investigator effects, the progress of incubation and chick development was observed from a distance of 20–40 m by binoculars. Every nest site was checked 1–3 times a week, depending on accessibility due to water level or fallen logs. In 1998, some nests were subjected to two additional approaches to capture and bleed hoatzin chicks. Nest sites were divided into those exposed to tourism and undisturbed nests situated in backwater and off-limit zones (Fig. 1).

2.3.2. Reproductive success

Calculation of nesting success and statistical comparison of undisturbed nests and tourist-exposed nests followed Mayfield (1961) and Hensler and Nichols (1981). We analysed incubation and chick period separately because tourist activity may influence breeding success in a different manner during different nesting stages. This also allowed us to include nests in the analysis for which only the fate of birds during one of these periods was known. We considered nests successful if at least one chick hatched after the incubation period or if at least one young had fledged after the fledging period, respectively. To determine the most vulnerable time during the fledging period, we further employed a life table analysis (SPSS 11.5) for the chicks.

To assure comparable conditions of nest sites with respect to climate, vegetation and tourist load only the first annual breeding attempt of a hoatzin pair was included in the analysis. Neither growth rate nor mortality differed between male and female chicks (results of molecular sexing; A.M., K.E.L., and M. Wink, unpublished) and thus sex was ignored in our analysis. Hoatzins are cooperatively breeding birds and group size is known to influence nesting success (Strahl, 1988). However, group composition was indistinguishable in undisturbed and tourist-exposed territories. In particular, the percentage of single pairs, which are the least successful, was similar in both samples with 19% and 20%, respectively (A.M. and K.E.L., unpubl. data).

2.3.3. Hormonal stress response of hoatzin chicks

In 1998, we measured the plasma concentrations of corticosterone to investigate if young hoatzins were physiologically stressed by tourism activities. We followed the capture stress protocol of Wingfield et al. (1983) which uses capture and handling as a standardised stressor and measures the increase of plasma corticosterone in subsequent blood samples. This method provides information about the sensitivity of the hypothalamo-pituitary-adrenal (HPA) axis and can reveal how an individual might be affected by other stressful stimuli, such as disease or human disturbances (Wingfield et al., 1995). In contrast, basal corticosterone levels only present the bird's current hormonal status.

We sampled hoatzin chicks at an age of 8–18 days when they remain quiet in the nest (nestlings) and as young birds at an age of 40–57 days that had already left the nest but prior to fledging (juveniles). The chicks were caught by hand directly from the nest (all nestlings) or from the branch where they were resting (juveniles). Some chicks jumped into the water when approached and were immediately caught with a fishing net. All stress protocols were carried out between 0900 and 1200 by the same researcher (A.M.). Sample time started (1) when the nesting tree was reached with the canoe or (2) at the moment when the young tried to escape before the canoe had reached the tree. This situation mimics the approach by a tourist group to the nesting site. The first bleeding occurred as soon as possible after capture ("initial sample"). Blood was collected from the wing vein into heparinised capillary tubes, ca. 50 μl/sample. Subsequent blood samples were taken at 10, 20, 35 and 70 min after the first sample. Between blood sampling events, the birds were guarded in cloth bags. After the final bleeding, individuals were weighted with a Pesola spring balance, colour banded and released at the place where they had been caught. The survival of sampled chicks was within the range of survival of birds that were not sampled.

The blood was stored on ice up to 6 h and then centrifuged with a hand centrifuge (3 min at 3000 rpm). Plasma was extracted with a Hamilton syringe and the volume was measured. The plasma was stored in 0.5 ml 100% ethanol (Wikelski et al., 2002) at 4 °C for several months and transported to the University of Illinois, where it was kept at −20 °C until analysis in 2000. Corticosterone was analysed by radioimmunoassay after extraction of corticosterone with dichloromethane (described in detail in Wikelski et al., 2000). Each sample was assayed in duplicate with a small amount of radiolabelled steroid added to determine recovery. The intra-assay variation was 9%, the inter-assay variation 12.5% and assay sensitivity was at 3 ng/ml. Differences in the stress response between tourist-exposed and undisturbed nest sites were compared by repeated-measures ANOVA. In juveniles the variances of the last sample (70-min sample) failed to be homogeneously distributed, but the variances were not correlated with the means and the F-statistic is known to be quite robust to a violation of this assumption. For several initial bleedings sampling time was delayed. To calculate true basal concentrations we therefore split the initial samples into those taken before and after 3 min after capture as 3 min is a common threshold for detecting stress-induced corticosterone secretion (M. Romero, unpubl. data).

To further test for associations between age or body weight and stress response, we calculated the maximum level of corticosterone achieved during the restraint, regardless of sample time and used Spearman's rank-order correlation. No sex differences existed in the stress response or body weights of sampled chicks, thus sex of the young was ignored in the analysis. There were three sibling pairs in each nestling group and two pairs in each of the juvenile groups. Because there was as much variation between siblings as there was between unrelated chicks (from different nests), the stress responses of all siblings were included in the analysis. We tried to sample the same individuals both as nestlings and as juveniles but were not successful in all cases. Thus, we included additional juveniles (not sampled as nestlings) in the analysis.

2.3.4. Flight behaviour of incubating hoatzins

We used flight distances of incubating hoatzins as an indicator of the behavioural response towards humans, assuming that the reactions to the investigator's canoe were at least as strong as to a bigger tourist boat with several people inside. In 1996 and 1997, hoatzin nests were approached approximately at a 45° angle to the shore line until the incubating bird was flushed away. The distance between boat and nest was measured with a range-finder to the nearest metre. The bird normally waited in a nearby tree and returned a few minutes later when the observer was outside the critical flight distance. We restricted experimental flushing to the period between week 2 and 4 of incubation (i.e., before the chicks start to hatch) to prevent abandonment of incubated nests and because flight distances might change during the nesting cycle. Every territory was considered only once and flight distances measured in 1996 and 1997 were combined. Comparisons of distances at undisturbed and at tourist-exposed nest sites were made by t-test.

3. Results

3.1. Breeding success

A total of 131 undisturbed nests and 83 tourist-visited nests were monitored during incubation of eggs and 74 and 61, respectively, during fledging (Table 1). Nest survival during the incubation period was similar at 23–28% for undisturbed and for tourist-exposed nests over the three years (Table 1). However, nest survival during the fledging period was always higher in undisturbed nests compared to tourist nests. This difference was most pronounced in 1996, also significant in 1998, but supported only by a weak trend in 1997. The survival functions for the chicks (Fig. 2) revealed that the lower survival of tourist-exposed chicks was due to a higher mortality in weeks 3–6 when the chicks had left the nest.

3.2. Hormonal response and body weight of hoatzin chicks

Hoatzin chicks at both undisturbed and tourist-exposed nests responded to our experimental capture and handling by a rapid increase in secretion of corticosterone. Maximum values were reached at 10–20 min of restraint and followed by a decrease, but even 70 min after capture the concentrations were still higher than initially. Among nestlings, the magnitude and pattern of this response was indistinguishable between undisturbed and tourist nests (Fig. 3(a); $F_{1,25} = 0.90$, $p = 0.35$, Table 2). Among juveniles, however, patterns of corticosterone secretion were strikingly different between individuals from undisturbed and from tourist-exposed nests (Fig. 3(b), $F_{1,19} = 8.53$, $p = 0.01$). Levels in tourist-exposed juveniles showed a much stronger increase within the first 20–30 min after capture and stayed at that level for more than 1 h, while previously undisturbed juveniles secreted less corticosterone and had already decreased plasma concentrations at the end of the stress protocol. Maximal corticosterone titres of the tourist-exposed juveniles were twice as high as those from birds living at undisturbed sites (Table 2).

Initial corticosterone levels were similar for hoatzin chicks from undisturbed and from tourist-exposed nests, for nestlings and for juveniles (Table 2). Baselines values, only from samples taken within the first 3 min after

Table 1
Success of hatching and fledging of hoatzins from undisturbed nests (U) and from tourist-exposed nests (T)

Year	Exposure (days)	Successful nests	Unsuccessful nests	Daily survival	Survival for entire period
1996					
Incubation					
U	339	7	14	0.9582	0.26
T	338	10	16	0.9573[a]	0.25
Fledging					
U	399	9	4	**0.9900**	0.57
T	338	3	11	**0.9638**[b]	0.13
1997					
Incubation					
U	822	15	32	0.9611	0.28
T	364	8	16	0.9560[c]	0.24
Fledging					
U	892	18	6	0.9933	0.69
T	567	8	8	0.9859[d]	0.46
1998					
Incubation					
U	968	20	43	0.9556	0.23
T	538	12	21	0.9610[e]	0.28
Fledging					
U	1183	22	15	**0.9873**	0.50
T	734	9	22	**0.9700**[f]	0.19

A successful nest produced at least one hatchling after the incubation period (32 days) or one fledgling after the fledging period (55 days), respectively. p levels are two-tailed. Bold print indicates significant results.

Incubation: [a]$Z = 0.17$, $p = 0.87$; [c]$Z = 0.40$, $p = 0.35$; [e]$Z = -0.50$, $p = 0.31$.

Fledging: [b]$Z = 2.21$, $p = 0.027$; [d]$Z = 1.30$, $p = 0.096$; [f]$Z = 2.44$, $p = 0.01$.

capture, were at 3.3 ± 0.73 ng/ml for the pooled nestlings ($n = 8$) and were similar for juveniles (3.8 ± 0.81 ng/ml, $n = 6$). These basal values were lower than the initial samples indicating that the latter include chicks that had already rapidly increased their corticosterone secretion after the first three minutes. For the graphic presentation in Fig. 3 the initial samples are therefore divided into those taken within and after the first three minutes. Thus, six sample groups are shown instead of the five considered in the ANOVA.

Body weights of nestlings were lower in the undisturbed group than in the tourist-exposed group, but this may have been because there was a suggestion that the sample of undisturbed individuals was slightly younger than the tourist-exposed one (Table 2). We found no correlation of maximum corticosterone values with body weights (undisturbed: $r_s = 0.14$, $p = 0.58$; tourist-exposed: $r_s = 0.35$, $p = 0.35$) or with age for both nestling groups (undisturbed: $r_s = 0.003$, $p = 1.0$; tourist-exposed: $r_s = 0.25$, $p = 0.51$). In contrast, juveniles from undisturbed nests had significantly higher body weights than juveniles from tourist-exposed nests, although the former were not older (Table 2). There was no association between body weight and maximal corticosterone values, either for undisturbed ($r_s = -0.03$, $p = 0.92$) or for tourist-exposed individuals ($r_s = -0.47$, $p = 0.20$). Interestingly, we detected a negative relationship of maximal corticosterone values with age only for tourist-exposed juveniles: older juveniles responded less to acute stress ($r_s = -0.72$, $p = 0.03$) whereas undisturbed juveniles did not show this relation ($r_s = -0.19$, $p = 0.56$).

3.3. Flight reactions of incubating hoatzins

Incubating hoatzins differed strikingly in their flushing distances, depending on whether they inhabited an undisturbed territory or a site with tourism activity (Fig. 4; $t = -5.6$, $p < 0.0001$). Hoatzins at undisturbed nests left their clutches much earlier when approached by a human compared to their conspecifics at tourist-exposed nests.

4. Discussion

4.1. Hoatzin reproductive success

Breeding success of hoatzins was higher at undisturbed nests than at tourist-exposed nests. This difference was solely due to an increased mortality of young birds prior to fledging whereas the success of incubation was similar in both groups. The effect fluctuated in its magnitude among years and seemed to be associated with the number of visitors and boats during the fledging period (Table 3). We suggest that the direct influence

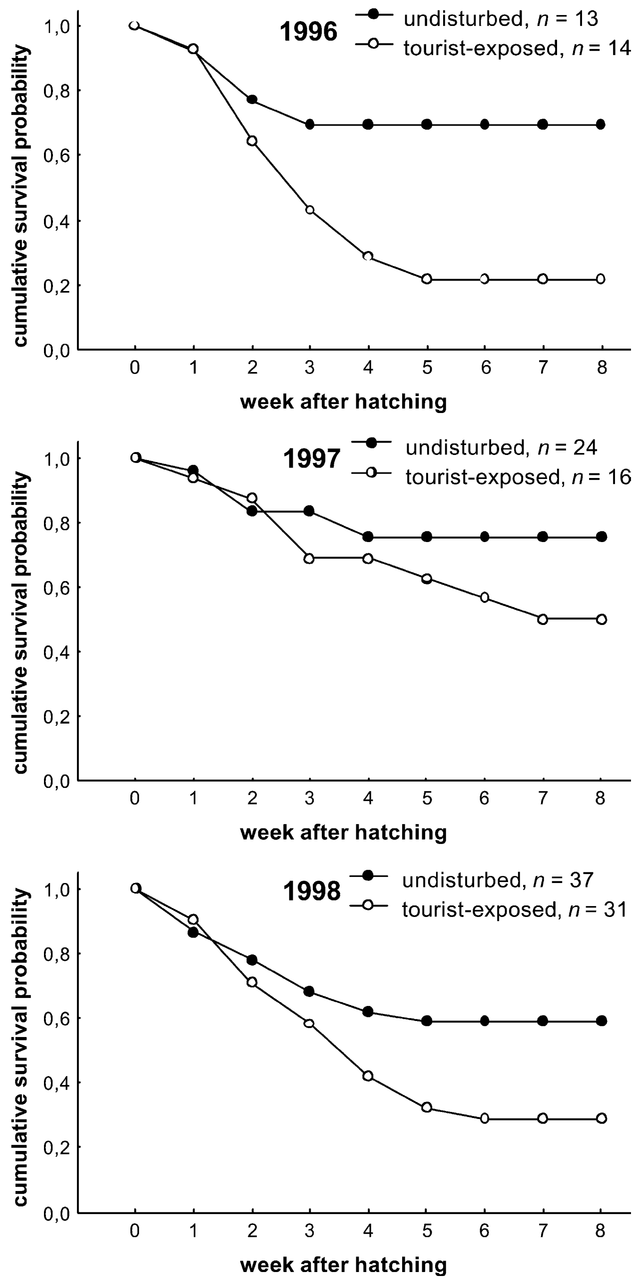

Fig. 2. Survival function of hoatzin chicks at undisturbed nests and at tourist-exposed nests. Functions differ significantly between undisturbed and tourist-exposed chicks in weeks 3–7 of chick development. Wilcoxon (Gehan) test 1996: 4.47, $p = 0.03$; 1997: 4.34, $p = 0.04$; 1998: 5.19, $p = 0.02$.

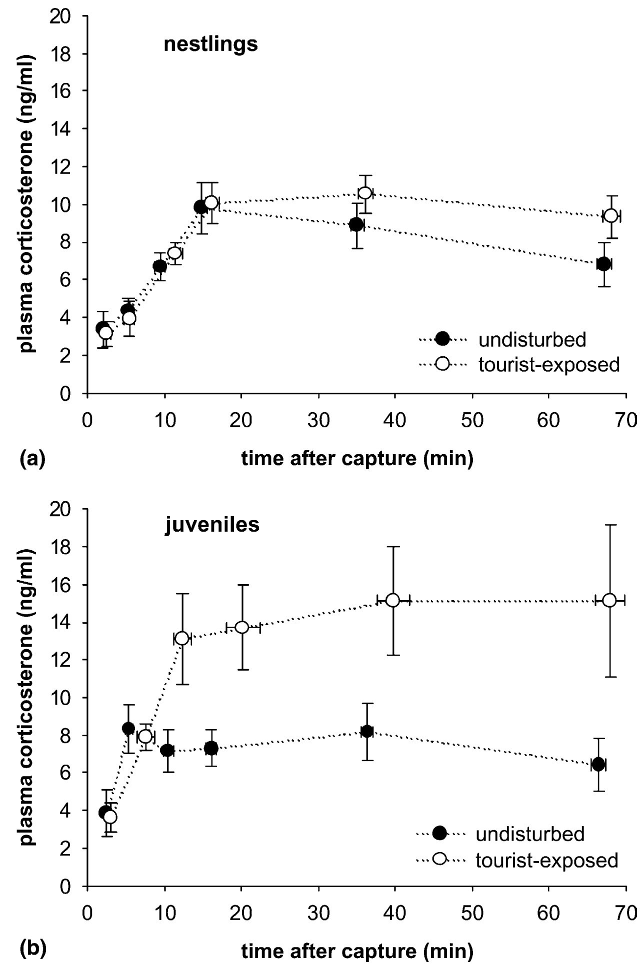

Fig. 3. Stress-induced corticosterone secretion of hoatzin chicks from undisturbed and from tourist-exposed nests. Each point represents the mean ± SE for the concentration of plasma corticosterone and sampling time for (a) $n = 18$ and 9 nestlings from undisturbed and tourist-exposed sites, respectively and (b) $n = 12$ and 9 juveniles from undisturbed and tourist-exposed sites, respectively.

of tourism activities are to blame for the observed higher mortality of hoatzin chicks in tourist-exposed areas and we suggest that the temporal overlap of the tourist high season in July and August with the hoatzin fledging period may be crucial for that impact. Diurnal predators were not more abundant at tourist-exposed territories and there is no evidence that differences in predation pressure could be responsible for the reduced chick survival of only tourist-exposed nests. The finding that nest survival during incubation was the same for all nest sites supports this conclusion.

Negative influences of human activities on development and survival of offspring are also reported for shore breeding and sea birds and have been linked to increased vigilance and reduced feeding rates (Safina and Burger, 1983; Flemming et al., 1988; Hatchwell, 1989). Other studies, however, showed effects of tourism activity on breeding success mainly during the incubation period (e.g., Anderson and Keith, 1980; Pierce and Simons, 1986; Keller, 1989). The fact that hoatzin hatching success was not affected by tourist-exposure might be explained by the apparent habituation of adult incubating hoatzins. The low tourist numbers in May and June may additionally aid in reducing an impact on incubation success.

The survival functions of chicks demonstrate that tourist chicks die more readily during the second part of

Table 2
Plasma corticosterone concentrations prior and in response to experimental stress and body condition of hoatzin nestlings and juveniles from undisturbed nests and tourist-exposed nests in the Cuyabeno Lakes in 1998

	Initial corticosterone (ng/ml)	Max. corticosterone (ng/ml)	Age (days)	Body weight (g)
Nestlings				
Undisturbed, $n = 18$	4.02 ± 0.55	12.69 ± 1.32	11.3 ± 0.6	83.6 ± 4.4
Tourist-exposed, $n = 9$	3.76 ± 0.75	12.02 ± 0.93	13.4 ± 1.1	119.22 ± 6.8
Significance p	0.78	0.74	0.08	0.0002
Juveniles				
Undisturbed, $n = 12$	6.82 ± 1.11	10.55 ± 1.17	47.7 ± 1.2	371.9 ± 12.9
Tourist-exposed, $n = 9$	6.94 ± 0.85	21.23 ± 3.73	46.1 ± 1.9	314.8 ± 17.2
Significance p	0.94	0.006	0.46	0.014

Results are given as arithmetic means ± SE. Comparisons were made by *t*-test, after verifying the normal distribution of the data by K–S test. Only age and body weight of nestlings were compared by Monte Carlo simulations (100,000 permutations) because data failed to be normally distributed.

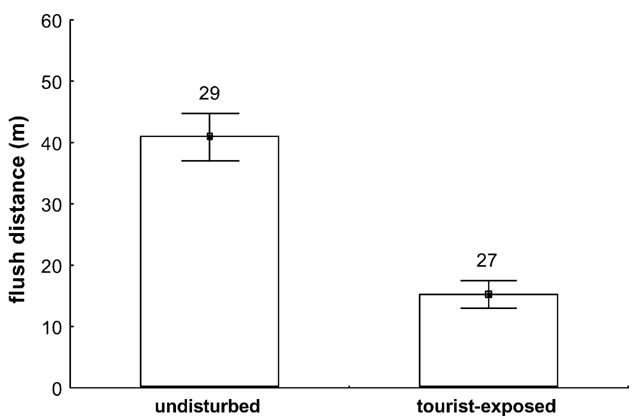

Fig. 4. Average distances at which incubating hoatzins flushed from the nest in response to an approaching observer. Whiskers represent SE; sample size is indicated above.

the fledging period. In this period chicks have already left the nest and are climbing through the foliage. Although juveniles are guarded by their parents most of the time they are also found alone. Especially when the family group has been flushed away juveniles prior to fledging cannot follow and have to rely on their unusual escape behaviour. In fact, we have evidence that juveniles were disturbed more frequently at tourist-exposed sites compared to undisturbed sites: on several occasions we found them resting on another tree than their initial nesting tree. This change of location involves swimming which is only elicited when the individual feels severely threatened.

When only undisturbed sites are considered the overall survival for both the incubation and the fledging period ranged between 0.12 and 0.19 in all study years (survival for entire incubation period and the entire fledging period, see Table 1). These values lie below values reported for other regions (22–27%, Ramo and Busto, 1984; Strahl and Schmitz, 1990; Domínguez-Bello et al., 1994). However, these authors calculated only simple percentages of successful nests instead of the more appropriate Mayfield estimates, which are known to be lower and avoid overestimating success due to nests found late in the season (Mayfield, 1961). In addition, previous studies were conducted in Gallery forests of the Llanos of Venezuela, while the Cuyabeno Lakes are embedded within a huge area of relatively pristine rainforest, where environmental factors including higher predation may contribute to a relatively low overall success.

4.2. Hormonal response of chicks to experimental stress

In response to a standardised stressor (capture) both hoatzin nestlings and juveniles showed the expected increase of the plasma corticosterone concentration (Wingfield et al., 1998), with initial and maximal values falling well within the range reported for other bird species (Romero et al., 2000). However, non-fledged

Table 3
Number of tourist boats and visitors during the breeding season of the hoatzins as well as nest survival during the fledging period in the Cuyabeno Lakes from 1996 to 1998

Year	Incubation period (May–June)		Fledging period (July–August)		
	Boats	Visitors	Boats	Visitors	Chick survival
1996	80	538	207	1461	0.13
1997	53	310	147	938	0.46
1998	82	470	188	1298	0.19

Data are based on the visitor registration at the reserve entrance to the Cuyabeno Lakes by the reserve administration of INEFAN.

juveniles from tourist-exposed nests responded much more strongly, showing higher maximum corticosterone values and a longer maintenance of the increased values. Thus, tourist-exposed juveniles demonstrated a higher sensitivity of their HPA axis to stressful events, which in vertebrates is known to be modulated based upon previous exposure to stressful stimuli like environmental stress or food conditions (Smith et al., 1994; Romero and Wikelski, 2001; Wikelski et al., 2001). Our results suggest that juvenile hoatzins experience tourist approaches as stressful and in consequence are sensitised by frequent visits. The hormonal response of nestlings, in contrast, was similar in individuals from undisturbed and from tourist-exposed nests indicating that tourism did not affect them measurably. These findings are highly consistent with the survival functions of the chicks, indicating that juveniles were in a particularly vulnerable life stage.

Fowler (1999) demonstrated that simple human presence at nest sites increased corticosterone concentrations in breeding Magellanic penguins (*Spheniscus magellanicus*) that are not accustomed to seeing humans, while birds exposed to high levels of human visitation did not respond to human presence as a stressor. Romero and Wikelski (2002) recently found similar results for Galapagos marine iguanas (*Amblyrhynchus cristatus*). However, penguins exposed to moderate levels of human disturbance did not show evidence of habituation over a period of several years and reacted with the same strong hormonal responses as entirely undisturbed birds (Fowler, 1999). In our study, tourist-exposed juveniles did not just react as strongly as undisturbed birds, but instead showed a much stronger corticosterone response. Such a sensitisation in the birds' response suggests that they had perceived the previous exposure to tourists as a stressful stimulus. Because the initial concentrations of plasma corticosterone were similar in juvenile hoatzins between undisturbed and tourist-exposed nest sites, tourism apparently did not result in chronically increased levels of corticosterone. However, it has to be considered that our juvenile sample is naturally biased towards surviving individuals who were able to cope with stress.

We could not detect a relationship between body weight and the hormonal stress response, either in nestlings or in juvenile hoatzins, which is consistent with data from other birds prior to fledging (Schwabl, 1999; Sims and Holberton, 2000). Thus, the strength of the hormonal reaction of the tourist-exposed juveniles cannot be explained by their lower body weights. On the contrary, we hypothesise that the lower body weights of tourist-exposed juveniles could most likely be a result of repeatedly elevated levels of corticosterone, which in turn are known to metabolise fat and protein reserves (Remage-Healey and Romero, 2001). Even if only one tourist boat per day elicits hormonal stress reactions, juveniles would accumulate a considerable number of such disturbance events in the weeks after they had left the nest. A reduced chick growth as a consequence of human presence could also be caused by reduced feeding rates by disturbed adults as documented for marsh harriers (*Circus aeruginosus*) (Fernández, 1993). This might apply to the hoatzins too, but the foraging bouts of the adults take place mostly in the morning and evening, avoiding the main visiting hours.

4.3. Habituation versus the maintenance of wariness

Adult hoatzins incubating their clutches tolerated human presence at tourist-exposed nests to a much higher degree than their conspecifics in undisturbed territories. In contrast to their offspring, they apparently habituated towards human observers. This allowed them to continue incubation while at the same time preventing the exposure of nests to predators and explains why hatching success is indistinguishable between undisturbed and tourist-exposed nest sites. The suppression of flight reactions as a result of habituation to recreational activities is known from other bird species too (Keller, 1989; van Heezik and Seddon, 1990; Yorio and Boersma, 1992). However, for the hoatzins in the Cuyabeno Lakes it remains unclear whether the observed individuals had truly habituated to tourism activities, or whether tourism had instead driven away particularly sensitive individuals with intrinsically high flight distances (Gutzwiller et al., 1998; Fernandéz-Juricic, 2000; Rodgers and Schwikert, 2002).

The important question remains: Why do hoatzin chicks not adapt to "harmless" tourists? Regular handling, for example, habituated nestlings of night herons (*Nycticorax nycticorax*) (Parsons and Burger, 1982) and mallards (*Anas platyrhynchos*) (Heise, 1989). On the other hand, human activities near nest sites of gulls resulted in a stronger wariness of chicks (Burger, 1981). We expect the threshold for habituation to be much higher in non-flying hoatzin chicks than in adults because their predation risk is presumably much higher. A suppression of escape behaviour or a reduced wariness could have severe consequences when faced with natural predators, and may therefore be counter-selected. Because the primary rainforest at our study site possesses a full range of predators we doubt that this adaptation will take place. Recent studies clearly show that several constraints prevent some species in adapting to disturbances even if plasticity in flight behaviour exists (Griffin et al., 2000; Blumstein et al., 2003).

Summarising, our data demonstrate that wildlife observation in the rainforest is not as harmless as often promulgated. Even a low number of ecotourists may have considerable negative effects on animals. Thus, even 'non-consumptive' tourist activities should be carefully monitored and managed. Off-limit zones free of human disturbance must be an integral part for visitor management and represent an indispensable reference for how undisturbed conditions are. Birds in different life stages may be sensitive in different ways and conservation practices should consider the most vulnerable period. Area-specific guidelines for wildlife observation should be developed and promoted. Measuring hormonal responses to experimental stress has proved to be a rapid and cost effective correlate of survival probabilities. We suggest it as a useful tool to assess the stress-tolerance of birds under different human disturbances.

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