Effects of Unit Size and Territory Defense on Communal Nest Care in the Hoatzin (*Opisthocomus hoazin*)

ERIC A. VANDERWERF[1] AND STUART D. STRAHL[2]
[1]*Department of Zoology, University of Florida, Gainesville, Florida 32611 USA, and*
[2]*Wildlife Conservation International, New York Zoological Society, Bronx, New York 10460 USA*

Reproductive success is positively correlated with unit size in many communally nesting species (e.g. Reyer 1980, Koenig 1981; for reviews see Emlen 1984, Brown 1987). In Hoatzins (*Opisthocomus hoazin*), the increased production of young in larger units is also linked with faster growth rates and earlier fledging (Strahl 1988, Strahl and Schmitz in press). During the breeding season, Hoatzin social units cooperatively defend all-purpose territories. In this study we documented mechanisms by which the reproductive success of larger units might be increased, and we examined the effects of territoriality on communal nest care.

Our work was conducted from June through August, 1987, on Fundo Pecuario Masaguaral, a cattle ranch in the central llanos of Estado Guárico, Venezuela. Hoatzins on the ranch inhabited areas of gallery forest along permanent watercourses and seasonally flooded areas of scrubby savanna woodland. Nesting occurred in the wet season (May–October). Troth (1979) described the area in detail.

We observed eight Hoatzin social units. Each contained two to five birds. Three units contained no helpers, and five units contained an average of two helpers. We identified each unit by a three-letter code, and distinguished individuals by colored leg bands placed on the birds as fledglings. To distinguish unbanded individuals, we used the pattern of wear and emergence of tail feathers. We made observations from 10–12 m tower blinds, from a portable mesh blind on the ground, or one on an inflatable raft. We observed at each nest for 6–10 three-hour periods. To compensate for differences in behavior due to daily activity patterns or demand for food by the young, we observed each nest for proportionally equal periods at different times of day and at approximately the same chick ages.

Adult Hoatzins feed the young by regurgitating partially digested plant material directly into the mouth of the chick. Each feeding comprises a variable number of periods when the adult's head is lowered and the chick takes all the food present in the adult's beak. The periods are of approximately equal length and occur at regular intervals. We recorded the total time adults spent feeding the chicks rather than just the feeding rate. Feeding data from chicks older than ca. 15–16 days were excluded because after this age the young were often out of the nest and not always visible.

We calculated *total feeding time* for each observation period by adding the lengths of all feedings by all birds in a unit during that observation period. Feeding time increased with brood size. To make between-unit comparisons of care delivered to each chick, we divided the total feeding time by brood size, yielding a *brood-size corrected feeding time.* Unit size and brood size remained constant for all units throughout the season.

We used percent attendance and average time per 3-h watch spent feeding young as measures of reproductive effort for individual birds. *Percent attendance* was measured as the proportion of total observation time that a bird incubated or brooded.

A *territorial dispute* was defined as any occasion on which the behavior of one group was disrupted by another. Length of territorial disputes was measured from the first alarm call to the return to previous behavior.

Attendance was inversely related to number of territorial disputes (Table 1, $P = 0.005$). Unit size was positively but not significantly correlated with number of territorial disputes (Table 1, $P = 0.13$).

Breeding females in units with helpers ($\bar{x} \pm$ SD = 47.0 ± 17.7%) were less attendant than those in units without helpers ($\bar{x}$ = 80.9 ± 17.1%) ($P = 0.05$, two-tailed Mann-Whitney *U*-test). The amount of time breeding females fed young in units with helpers ($\bar{x}$ = 9.75 ± 5.58 min per 3-h period) was also lower than in units without helpers ($\bar{x}$ = 10.13 ± 4.11 min per 3-h period), but the difference was not significant (P = 0.10, two-tailed Mann-Whitney *U*-test). In contrast, breeding males showed no significant differences in attendance or in amount of time spent feeding the young in units with and without helpers (two-tailed Mann-Whitney *U*-test).

Brood-size-corrected feeding times in units with helpers were higher than those in units without helpers (Table 2, $P = 0.005$, independent samples, two-tailed *t*-test). Chicks in units with helpers received more food than those in units without helpers.

Unit size and number of territorial disputes had significant and opposing effects in a multiple-regression analysis of total feeding time (partial $t = 2.90$, $P = 0.008$, partial $t = 2.27$, $P = 0.033$, respectively). Brood size was a significant predictor of total feeding time (partial $t = 3.08$, $P = 0.005$), but was not significant in a similar analysis of corrected feeding time (partial $t = 0.36$, $P = 0.73$). Chick age and time of day had no significant effects on total feeding time (partial t = 0.51, $P = 0.62$, partial $t = -0.05$, $P = 0.96$, respectively).

Energetic considerations may be especially important in the Hoatzin because of its lower-energy diet

TABLE 1. Spearman correlation of unit size, attendance, number of territorial disputes, corrected feeding time, and total feeding time. * = $P < 0.05$.

	Unit size	Attendance	No. of terr. disp.	Cor. feed. time
Unit size	—			
Attendance	−0.52	—		
No. of terr. disp.	0.58	−0.87*	—	
Cor. feed. time	0.35	0.07	−0.12	—
Total feed. time	0.36	0.05	−0.10	0.86*

TABLE 2. Unit size, brood size, corrected feeding time in min per 3-h observation period, percent attendance, and number of territorial disputes per 3-h observation period, by unit.

Unit	Unit size	Brood size	Cor. feed. time	Nest attendance (%)	No. of terr. disp.
CTU	2	1	6.38	100.00	0.00
PRC	2	2	7.90	100.00	0.00
SUK	2	2	8.38	99.49	0.36
OMY	3	3	7.19	97.14	0.57
CRO	3	3	13.31	100.00	0.00
NLI	4	2	17.12	99.14	0.33
SPL	5	2	7.17	95.00	1.12
DNS	5	2	14.65	99.79	0.36

(Morton 1978). The amount of food delivered to the young may be limited more by the parent's ability to digest plant material than by the time required to gather food (Grajal et al. 1989). After foraging, Hoatzins often sit so that the weight of the distended crop rests on the large epidermal callosity on the posterior tip of the sternum. Birds in this position sometimes remain motionless for more than an hour at a time.

The Hoatzin may be predisposed to communal breeding by its unusual diet. We found that helpers, by increasing the amount of food supplied to the young, may increase the reproductive success of the unit (Reyer 1980, Koenig 1981, Woolfenden and Fitzpatrick 1984). Increased food delivery may be responsible for the rapid development and earlier fledging of chicks in larger units, which may lead to decreased predation, earlier independence, and even larger adult size (Lack 1968: 171, Ricklefs 1976). Higher chick survivorship and possibly greater reproductive viability constitute an increase in inclusive fitness for the breeding pair and helpers (Brown and Brown 1981, Brown 1987).

One unit, OMY, had a lower corrected feeding-time value than expected for its unit size (Table 2). Unit OMY was atypical because it consisted of only one male and two females but contained two clutches of eggs. This was the only case of polygamy at the study area. One female became dominant by the brooding stage and rarely allowed the second female to brood or feed the young. Unit OMY had a functional unit size of only two when the feeding data were taken. This pairing resulted in frequent parental conflict that reduced attendance. Both females functioned as breeder and helper, but we considered the dominant female as the breeder and the subordinate female as the helper.

Attendance in units with helpers ($\bar{x} = 98.21 \pm 2.12\%$) was lower than in units without helpers ($\bar{x} = 99.83 \pm 0.29\%$) (Table 1). We expected larger units to show higher attendance because more members could share the work. However, larger units engaged in more territorial disputes (Table 2), and all other behavior ceased during territorial disputes. Birds that were incubating, brooding, or feeding young would usually leave the nest to join in the defense. It took several minutes for birds to settle down after a territorial dispute and resume their previous activity. Consequently, larger units actually devoted less time to attending the nest. Unit SPL represented an extreme example. It maintained a very large territory in one of the areas most densely inhabited by Hoatzins, and it spent significantly more time in territorial defense than did other units (Table 2, $P = 0.002$, independent samples, two-tailed t-test). Thus, the compromise between the costs of territoriality and the benefits of helping in Hoatzins may place an upper limit on unit size. This may be a general mechanism determining unit size in many communally nesting birds.

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