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Observations on the breeding biology of the Writhed-billed Hornbill (*Aceros waldeni*) in the Philippines*)

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Summary

We report on some aspects of the breeding biology of the critically endangered Writhed-billed Hornbill (*Aceros waldeni*) on the island of Panay, Philippines. Observations were made at three nests during 1995–1997. Walling-in of the females commenced in the first week of March. One female remained incarcerated for 77 days, two of three broods completed fledging around May 20 (1995, 1997). Details on fledging of the female and her brood and postfledging care by both parents are reported.

The food of the males at two nests was ca. 98% fruits and 2% invertebrates. The plants exploited comprised at least 14 species. Over a third of the fruits delivered were figs of a small number of species.

Two males had average feeding rates of 0.56 and 0.88 times per hour respectively, and fed 1 to 66 (median 8) items per feeding visit at the nest. The hourly feeding rate increased after hatching, but the composition of the diet did not change noticeably. As a rule, food items were delivered singly and, during one visit, in runs of one, or rarely up to 3, species.

In the three weeks following vacation of the nest, the male appeared to be the sole food provider while the female stayed continually with the 3 young (as sentinel?) in the vicinity of the nest.

The nest environs were defended by the male against Tarictic Hornbills (*Penelopides panini panini*). Six vocalisations of the parents are mentioned. One was used in territorial skirmishes with Tarictic Hornbills.

With perhaps less than 30 pairs of the Writhed-bill surviving, the future for the species looks bleak. Only drastic conservation measures can prevent the species' demise. Some have been started by the PESCP.

Key words: breeding cycle, diet composition, parental behaviour, territoriality, vocalisations

Zusammenfassung

Beobachtungen zur Brutbiologie des Runzelhornvogels (*Aceros waldeni*) auf den Philippinen

Wir berichten über einige Aspekte der Brutbiologie der stark vom Aussterben bedrohten Hornvogelart *Aceros waldeni* auf der philippinischen Insel Panay. Die Ergebnisse stammen aus Beobachtungen an drei Bruten von 1995 bis 1997. Das Weibchen mauert sich in der ersten bis zweiten Märzwoche ein und bleibt im Nest, bis die Jungen ausfliegen (20. Mai). Das Männchen füttert am Nest durchschnittlich 0,56- bis 0,88mal pro Stunde und 1 bis 66 (Median 8) Nahrungsstücke pro Fütterung. Die verfütterte Nahrung besteht zu ca. 98% aus Früchten und zu 2% aus wirbellosen Beutetieren und wird in der Regel einzeln Stück für Stück übergeben. Dabei wird bei einem Nestbesuch meist nur eine Nahrungsart (selten bis zu 3) überreicht. Das Männchen war bei einer Brut auch nach dem Ausfliegen der Hauptversorger, während das Weibchen stets bei den Flügglingen blieb. Das Revier-Männchen ist gegen Tariktik-Hornvögel territorial. Altvögel äußern wenigstens sechs Lauttypen, deren Kontext kurz beschrieben wird.

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Introduction

Two species of hornbills occur in the West Visayas in the Philippines: Visayan Tarictic Hornbill (*Penelopides panini panini*) and Writhed-billed Hornbill (*Aceros waldeni*), both of which must be considered as critically endangered (Collar et al. 1994). Whereas the Writhed-billed Hornbill was formerly regarded as a subspecies of *Aceros leucocephalus*, it is now regarded as a full species because of its different colouration and discrete range (Kemp 1995). It is confined to Negros and Panay and is probably extinct on Guimaras (Collar et al. 1994), owing to the almost complete deforestation of the island. On Negros, sightings have been scanty in recent years. Only one family of four was seen during 5 weeks of fieldwork (Evans et al. 1993), and during 15 months in the North Negros Forest Reserve a single male was encountered by a team belonging to our project in 1996. There was similarly a lack of sightings on Panay, so the species was considered to be close to extinction there (Evans et al. 1993). Recent observations contradict these assumptions: in 1994 there was a flock of 25–30 Writhed-billed Hornbills observed in a single fruiting tree near Dalagsaan, Aklan Province. This was the largest flock of the species ever recorded by European observers (Curio 1995). Since then two active nest holes were found in Hamtang Forest, Valderrama area, Antique Province in 1996, and five individuals (three males, two females) were seen there in 1995. One active nest was observed near Sibaliw, NW Panay peninsula in 1997 (Ballhaus in litt.). Conversely, more than 26 nests of Tarictics have been found in the Hamtang area (Curio 1996). Writhed-billed are thus outnumbered by Tarictics by a factor of 10 to 15.

Writhed-billed Hornbills are known to inhabit primary evergreen lowland forests up to montane forests. Their feeding and breeding biology are so far unknown (Kemp 1995). However, observations have been made by members of the "Philippine Endemic Species Conservation Project" (PESCP) of the Frankfurt Zoological Society. This paper deals with the results of a seven weeks observation period of a breeding pair in Hamtang Forest in 1996, with additional observations of the pair's male in 1995 and of another nest in 1997.

Methods

The study was mainly conducted from March to April 1996 in Hamtang Forest (11° 8' N, 122° 11' E), a primary forest at 950 m asl near Mt. Baloy (1729 m asl) on the island of Panay, Philippines. The area is uninhabited but suffers some disturbance by people.

Data were collected on 35 days between March 6 and April 27 1996. We watched a single nest for 2.5 to 6 hours during the daylight period (6 a.m. to 6 p.m.) for a total of 183.5 hours. Observations were made from a blind on the ground at a distance of 25 m from the nest tree, using 20× – 60× telescopes. Additional observations were made at the same nest in 1995 from March to early June by M. Doll and one of us (L. L. L.) (see 2nd Report of project, Curio 1996).

For each visit of the male at the nest, we noted the times of arrival and departure as well as the number and type of food items brought. Calls and other behaviours were also recorded.

Additional observations were made by M. Ballhaus (pers. comm.) at a second nest in May 1997. It was located in the submontane forest at our new camp site in Sibaliw, Municipality of Buruanga, on the Panay peninsula (11° 49' N, 121° 58' E, 450 m asl). The nest hole was in a strong branch about 20 m above ground in a ca. 25 m high tree on a ridge. The observation blind was placed 30 m away. The nest was found on May 8 but owing to the shyness of the attendant male and heavy rains, observations did not start until May 17. Apart from some data on feeding, date of fledging and the appearance of the young was recorded not until some days later. Observations lasted till August 8 when the family had gradually moved away from the nest tree.

Results

General observations

The Hamtang nest hole was located in a living Balak-bákan tree (*Shorea* [*polysperma*?]) at about 12 m above the ground and the opening slit was directed toward the southeast (140°). The same nest was occupied by a pair with the same male in the year before; the male was identified by a feather anomaly at its right carpal joint, as documented by photography.

At the beginning of the observations on March 5, the nest cavity was already closed by the

female, leaving only a narrow slit through which the male could feed her. Even though the nest entrance was already closed on our arrival, the female never stopped sealing. She used food remains and her own faeces for this purpose. In the year before, two females that had foraged in a fig tree nearby with three males ceased their foraging visits on March 7, i.e. apparently started their sealed-in phase of nesting.

To defecate, the female positions the anus at the slit of the sealing and squirts her excreta with much force. In most cases the entrance remains free from any droppings. When present, the remnants seem to be of drier consistence than usual. For further sealing, the female applies them with the flattened sides of the bill, rendering the edges of the slit thicker and thicker.

We also heard noises from inside the hole such as the sound made by the bird pecking the wood of the walls.

Males not only feed together, at least prior to the start of breeding, but also may roost together. On March 16, 1995, i.e. 10 days after the focal female had gone into seclusion, three males came flying from a fig tree to roost ca. 300 m away. A fourth male, probably the nest male, joined them as they passed the nest tree (Lastimoza & Doll 1995).

Feeding observations

The male feeds his mate or family several times a day. There were no family helpers to feed the female. Upon arrival, the male always stays a short while on some branch near the nest and utters soft contact calls before he clings to the entrance and starts feeding. This is done by regurgitating a fruit, then holding it with the extreme tip of the bill and passing it in to the female. In this way fruits are mostly fed singly; even when the male regurgitates several very small fruits at a time, the female usually takes them one by one. Twice the female tried to catch an insect flying in front of the slit, and in one case she succeeded.

During 183.5 hours of observation at the Hamtang nest, the male brought a total of 1505 food items, of which 96% were fruits, to the nest. In 96 of 103 recorded feeding visits only one type of fruit was delivered. Hence, the male likely fed on one tree at a time and returned to the nest before exploiting the next one. This probably prevents the fruit being digested before he reaches the nest to feed. When the male had been scared by an observer, it delayed a nest visit while flying around with threat calls (see below). On these occasions the male regurgitated only seeds and voided them without delivery, obviously after too long a time between foraging and feeding the female. The male then left the nest immediately to collect new food for the family.

Two percent of the diet was invertebrate prey such as snails, beetles and caterpillars, and 2% remained unidentified. Table 1 shows the detailed composition of the diet as delivered at the nest in detail. There was little variation in the composition of the food delivered to the female across the observation period (not illustrated). The number of items per visit that were given singly and in runs of usually one food species, ranging from 1 to 66 with a median value of 8 ($Q_1 = 4$; $Q_3 = 17.5$). The Sibaliw male mixed up to three fruit species in half of the small number of visits observed. Frequency of feeding varied during the course of the day (see Fig. 1). It was highest early in the morning between 6:00 and 8:00 h, then declined towards noon and increased again between 14:00 and 16:00 h. Figure 2 shows the daytime distribution of the amount of delivered food during the whole of the observation period. The highest rates during both a.m. and p.m. periods occurred after April 18 indicating that the young had hatched some time before (see Discussion).

At the Sibaliw nest, only scanty observations

Table 1. Diet of *Aceros waldeni* as delivered at the nest, 1996

Tab. 1. Von einem *Aceros waldeni*-Männchen am Nest übergebene Nahrung, 1996

Item	Number	Percent
Fruits	1453	96.6%
'dalakit' (Moraceae)[1]	501	33.3%
'buka-buka' (Pterocarpaceae)[1]	349	23.2%
'bakan' (Icainaceae)[1]	66	4.4%
other	537	35.7%
Invertebrate prey[2]	27	1.8%
Unidentified	25	1.7%
Total	1505	100%

[1] Fruits collected for identification, export permit still pending.

[2] Composition of the invertebrate prey: snails 56%, caterpillars 7%, others 37%

were made on the feeding by the male. Three days after the female's leaving the nest hole and two days after the second young had fledged, the male was habituated sufficiently to permit long-term observations to start on May 20. There were 15 nest visits by the male and one by the female between 5:35 and 17:00 h. During this time, visits occurred between 7:06 and 15:48 h, the one by the female at 14:06 h. Visits to the nest tree lasted from 1 to 6 min ($\bar{x}$ = 3.2 min, n = 9). There were three visits of the male without any delivery of food. Feedings comprised 1 to 10 items delivered to the remaining nestling ($\bar{x}$ = 5.4, n = 9). The male that usually arrived with multiple loads fed the items one at a time. In between, it flew to a vine above the nest hole to regurgitate the next item. Except for one insect, all food items delivered were fruits. For 6 visits the food could not be identified. Altogether 14 food plants were fed to their families by two males in Hamtang (1995, 1996) and Sibaliw (1997), including three not identified (App.). There may be many more, even not including the figs which may well exceed 30 species (A. Hamann pers. comm.).

Two days after, on May 22 (5:15 – 10:15 h), the male visited the nest tree repeatedly without any food between visits with food. The female did so once. By 11:15 h, the third nestling had left the nest and the family could be heard nearby. As in other altricial birds, parents may have enticed fledging by withholding food during visits that the nestling(s) could perceive well when perching in the nest entrance in the days prior to fledging.

The provisioning rate of the male when feeding the lone and third young to fledging was 0.88 h^{-1} (10 visits/11.42 h). Including the female's visit, the rate was 0.96 h^{-1}. This per capita rate was higher than the average visiting rate of 0.56 h^{-1} of the Hamtang male for the whole of its family (Fig. 1). When converted into a per capita rate, the Hamtang male ranked even lower; with perhaps two young (it had 3 in 1995), the per capita rate of nest visits fell to 0.19 h^{-1}. However, in terms of number of items brought per visit, the Hamtang male did better than the Sibaliw male. The latter delivered 5.4 items per visit when the number of items could be counted. By converting number of items per visit into number of items per hour one arrives at an estimate of per capita 4.75 h^{-1} for the Sibaliw male. Hence, this male ranked still higher by a factor of about 2 when compared with the Hamtang male that attained only 2.73 items h^{-1} per capita (1505 items / 183.5 h / 3 family members to be cared for). This difference was exacerbated by the Sibaliw male caring for the first and, perhaps, also for the second chick in the nest environs during observations. A number of uncertainties may affect this comparison, the size and/or quality of the food items may be the most significant, though the percentage of animal food does not appreciably differ (1.8% in Hamtang [Table 1] vs. 2.0% in Sibaliw). Real differences in male quality could not be excluded.

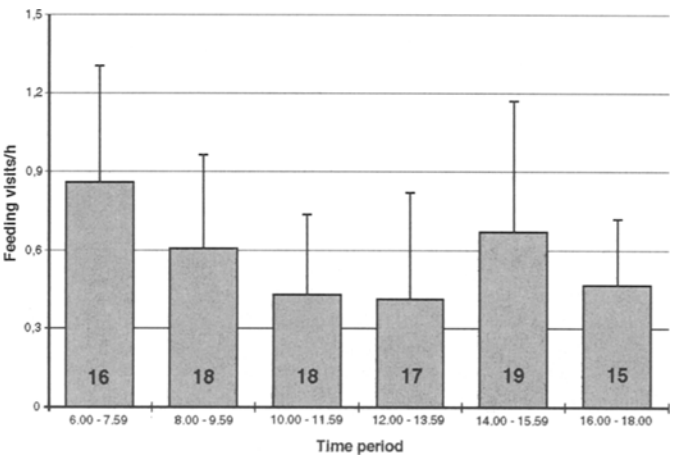

Fig. 1. Feeding frequency of a male *Aceros waldeni* during daylight. The columns show the average number of feeding visits per hour at the nest ($\bar{x} \pm$ s.d.).

Abb. 1. Fütterrate eines *Aceros waldeni*-Männchen bei Tageslicht. Die Säulen geben die mittlere Anzahl der Fütterbesuche/h ($\bar{x} \pm$ s.d.) am Nest an.

Fledging

On the day that observations at the Sibaliw nest started, i.e. in the morning of May 17, the female and two young could be seen at the entrance. By then one of the three young had left the nest and was moving around in trees nearby. In the afternoon the female was found outside the nest. By next morning, both young were peering out of the hole. Their naked faces were coloured greenish-yellow, similar to the male's naked facial skin, and also resembling two fledgling females described previously (Curio et al. 1996). The colour of the bill resembled the male's coral red, not the paler one of the female. The eye colour was **blue** not bright rufous as in the adult male. For a possible sex difference in fledgling eye colour see Curio et al. (in prep.).

The first chick fledged was seen only after leaving the nest before May 17. It differed from its sibs by having a grey head instead of the rufous-brown. Unfortunately, its eye colour went unseen. The second young fledged on May 19, i.e. one day after the female's breaking free, the third young in the morning of May 22 (see previous section). Prior to that date, the female may have been caring for the first two fledglings to judge by her very low feeding rate on May 20; one of 11 feeding visits to the nest had been by the female (see previous section). Alternatively, the female after ending her incarceration may be intrinsically less ready to provision her offspring. In *Aceros cassidix*, she contributes only 5% of the food needed by her one chick (Kinnaird 1996). There was no indication of any sealing of the nest entrance after the female's leaving the nest.

During the three weeks following vacation of the nesthole, the female and the three young moved around nearby. There was no indication that any of them had returned to the nesthole. The male appeared to do all the provisioning while the female possibly acted as sentinel; she always moved with her young. As the family explored the nest environs more widely, they were more often heard than seen. After June 12, the young were heard calling, on June 25 in a 'duck-like' fashion. At this time the young still had shorter tails than the parents. Following July 7, the female was more often seen in the company of one young whereas the latter moved also around singly. From that time the male was not seen again.

Territoriality

Aceros waldeni is a territorial bird at least for the breeding season. During our observations at the nest hole we could often hear the loud territorial call (see below). *A. waldeni* seems to behave agonistically especially towards Tarictic Hornbills, perhaps due to similar demands for nesting sites and fruit availability. Lastimoza & Doll (1995) observed a Writhed-bill chasing away a Tarictic that came to a fruiting 'Bantugan' tree at the same time. The chasing was accompanied by loud calls and vigorous wing-beats. The situation was the reverse the next morning when three Tarictics chased away the Writhed-bill from the fruiting tree.

Vocalisations

Six different types of vocalisation were heard from Writhed-billed Hornbills:

The territorial call is a loud and far carrying bleating "wah-ha-ha-ha", sounding very much like the bleating of a lamb.

Even louder is the threat call "yak-kak-kak-kak", uttered repeatedly when the male is scared by a human near the nest or is engaged in an agonistic encounter.

Near the hole, the male utters a soft croaking and babbling contact call or a monosyllabic "krook".

After the delivery of the food, the female answers the male's feedings with a subdued hissing.

When out of the nest, the female utters calls similar to the male's soft croaking calls ('krook') but at a higher pitch. These female calls were heard when the first of two young had left the nest and the female was paying short visits to the nest tree where the male was still feeding the other nestling.

Discussion

Aceros waldeni is a fruit-eater that takes a surprisingly small amount of invertebrate prey (ca. 2%), at least during the breeding season. At this time animal prey is of special importance to satisfy the increased demand for proteins by the laying female and growing chicks (Kemp 1995). A more detailed investigation of the quantity of invertebrates in the diet could only

be made by comparing several pairs, taking into account the profitability of the territory. However, the major part of the bird's breeding season diet (96 to 98%) was composed of different fruits, as found in two broods (1996, 1997). This holds true also for *Aceros cassidix* on Sulawesi, though 12% of the diet remained unidentified (Kinnaird & O'Brien 1993), but is in stark contrast to a captive breeding male *A. leucocephalus* taking a mere 20% fruit and 80% animal food (Myers submitted). It is difficult to believe that wild males are constrained in feeding that much animal food since pre-fledging development is more rapid rather than slowed down (see below).

With only 2% animal matter in its breeding season diet, the Writhed-bill undercuts the minimum known for four well-studied Asian hornbills. The proportion of animal food varies from 5.1% (*Rhyticeros undulatus*) to 40% (*Anorrhinus tickelli*) (Poonswad and Kemp 1993, see also Tsuji 1996). Visayan Tarictics living syntopically with Writhed-bills incorporate a markedly higher percentage of up to 12% of animal food in their provisioning diet (T. Hahn pers. comm., M. K. pers. obs., Klop 1998).

Leighton & Leighton (1983) reported six Bornean Hornbills to have a preference for lipid-rich fruits, as e.g. Myristicaceae, Meliaceae and Lauraceae; they tend to ignore sugar-rich fruits, such as figs. By contrast, Kinnaird & O' Brien (1996) report flocks of *Aceros cassidix* on Sulawesi moving around to exploit figs as they ripen. During breeding, figs constitute 70% of the food (Kinnaird & O'Brien 1993). Similarly, about one third of the food items brought to the Hamtang female were figs (i.e. sugar-rich fruits), and we repeatedly watched Hornbills feeding on fig patches before breeding. The preference for figs in these hornbills and other frugivores may well be due to the disproportionately high calcium content in this 'keystone' plant resource (O'Brien et al. 1998).

Although chicks hatched in the sixth week of our observation period in Hamtang forest, there was no noticeable change in the composition of the diet – although the actual species of fruits might have changed. There is some indication that upon hatching the feeding rate increased (Fig. 2). Whether there was a clear change of feeding rate in the course of the day (Fig. 1) cannot be ascertained, because records of feeding rates at different times of the day were not distributed evenly enough for statistical testing.

The fruits in the diet came from at least 14 plant species (App.), a figure that probably grossly underestimates what is really fed. Poonswad and Kemp (1993) listed up to 50 species in the diet of four Asian hornbills, and the Tarictic using the same habitat as the Writhed-bill exploits at least 30 species (Klop 1998).

Food was typically delivered in runs of items of one species, indicating that the male exploited one species of tree on each foraging trip. (A closely observed Tarictic male at Hamtang showed the same habit when delivering fruits in monospecific bouts of from 5 to 78 [Lastimoza & Doll 1995]).

Even after the young had fledged, the male at Sibaliw continued to be the main provider of food while the female stayed (as sentinel?) with the young (see also Myers 1998: *Aceros leucocephalus*).

The young developed rapidly. They took slightly over 40 days to fledging, assuming an incubation period of 29 days, as inferred from other *Aceros* with a similar female body mass (Kemp 1995, Table 5.1) While Kemp (1995) reported the female in *Aceros* to leave the nest before the young, the Sibaliw female left after the first of three chicks.

Cooperative breeding, as reported for *Aceros comatus* and for some other hornbill genera (Kemp 1995, Witmer 1993, Tsuji 1996), was not observed.

The breeding cycle can be reconstructed roughly: on March 5 1996, the nest cavity was already closed, indicating that the egg laying/incubation period had begun. Lastimoza & Doll (1995) reported March 6 as the beginning of the incubation period in the year before. As Kemp (1995) reported, the incubation time in the much larger *A. corrugatus* is 29 days but does not decrease rapidly with decreasing body weight. So it seems reasonable to assume 29 days for *A. waldeni*, too, in which case the chicks could have hatched in the first week of April, the time when the feeding rate increased. Maxima for both mornings and afternoons occurred after April 18. By then the young would have been at least one week old. As Lastimoza & Doll (1995) reported for that year, the young of the breeding *A. waldeni* pair in Hamtang

Forest fledged by May 22. For *A. leucocephalus*, being of about the same body size as *A. waldeni*, the nestling period is 92 days (Kemp 1995). Two more captive broods fledged after 59 to 66 days and 63 to 71 days, respectively (Myers 1998). However, such long periods may be an attribute of captive breeding. Moreover, the larger *A. corrugatus* (1273 g vs. 748 g female mass) was found to have a nestling period of only 63–73 days (Kemp 1995). Thus, it is reasonable to assume that *A. waldeni* has a nestling period of about 60 days or less. The Hamtang pair of 1995 demonstrates that this assumed period must be markedly undercut. The female went into seclusion on March 6 and the three young fledged exactly 77 days later (Lastimoza & Doll 1995). Given an incubation period of 29 days, the nestling period must have been as short as about 42, allowing for an egg-laying period of 6 days (Kemp 1995). The same male (and female?) had already begun their cycle in 1996 by March 5 and had not completed their cycle by April 27 (Fig. 2), when observations ceased. By analogy, the Sibaliw brood that fledged during May 17–22, 1997, would have started its cycle (walling-in) on about March 6, which is not too different from the start of breeding by the Hamtang pair in 1995 and 1996.

Fledging of chicks could have been influenced by the male, as suggested by his non-feeding visits to the nest tree (see also Tsuji 1996: *Buceros bicornis*) when only one young remained, two days after the second young had fledged.

Territorial behaviour of the Hamtang Writhed-billed male in 1995 was pronounced. It chased away up to two Tarictics (*Penelopides p. panini*) near its nest, but not when the latter outnumbered him by more. However, territoriality did not prevent a Tarictic pair from settling a mere 40 m away from the Hamtang pair in 1995. Whether fighting is over food or over nest holes is not clear since systematic observations in the non-breeding season are lacking. The interspecific hostility of the Writhed-bill

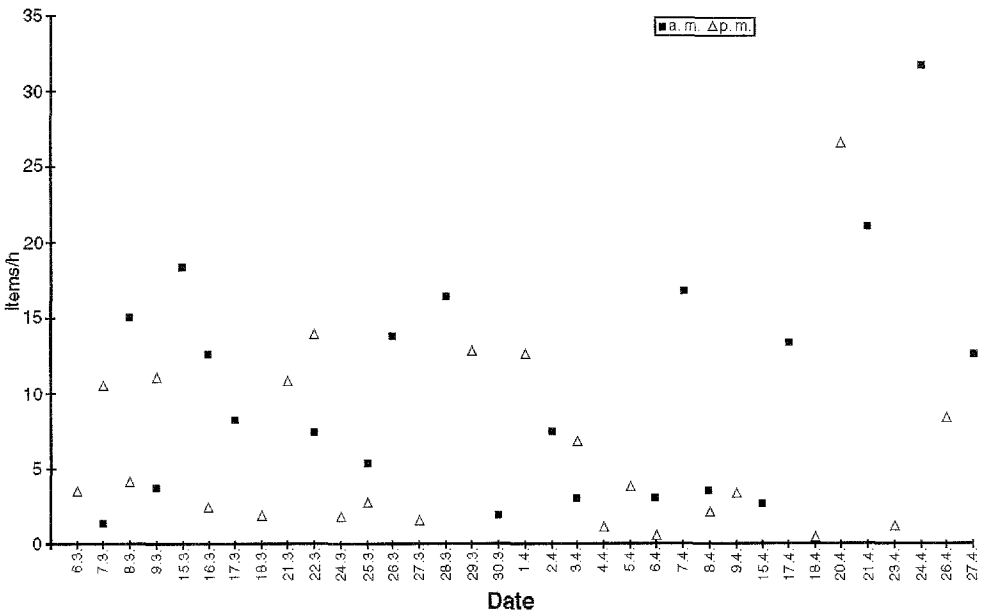

Fig. 2. Daily distribution of food delivered by a male *Aceros waldeni* during the nesting cycle in 1996. Symbols indicate the average number of food items per hour.

Abb. 2. Verteilung der von einem *Aceros waldeni*-Männchen am Nest während des Brutzyklus 1996 verfütterten Nahrung. Die Symbole geben die durchschnittliche Anzahl an Nahrungsstücken/h für vormittags (■) und nachmittags (Δ) an.

contrasts markedly with its tolerance vis-à-vis conspecifics when feeding in a fig tree. Up to three males and two females foraged there peacefully side by side on the days preceding the female's start of breeding in 1995. This is surprising since intraspecific competition is generally much more intense than interspecific competition.

Given the scanty data base of the present study, one cannot provide a generalized picture of the species' breeding biology. However, the study supplies the first information on the diet and breeding biology of *Aceros waldeni* and thus might contribute to the preservation of this critically endangered species. Based on a recent estimate of primary forest area in the Panay mountains (T. Hahn pers. comm., Klop 1998), suitable habitat for both *A. waldeni* and *Penelopides panini panini* may amount to nearly 500 km^2. Extrapolating from the ratio of Tarictics to Writhed-bills at Hamtang (see Introduction) to the whole of the Panay forest area, there may be as few as 25–30 pairs or, perhaps 100 pairs (Klop 1998) of Writhed-bills left on Panay. Numbers on Negros must be even far lower though precise estimates are lacking. Accordingly, *A. waldeni* is sadly one of the most endangered bird species in the world. The Philippine Endemic Species Conservation Project has launched an education campaign towards rescuing the species and its remaining habitat on Panay.

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References

Collar, N.J., Crosby, M.J. & Stattersfield, A.J. (1994): Birds to watch 2. The world checklist of threatened birds. Cambridge, UK.

Curio, E. (1995): Philippine hornbills. Hornbill Newsletter 1: 11.

Curio, E. (1996): Second Report, unpublished, of Philippine Endemic Species Conservation Project. Ruhr-Universität Bochum, Germany.

Curio, E., Hamann, A. & Lastimoza, L.L. (1996): The appearance and status of Writhed-billed Hornbill *Aceros waldeni* on Panay. OBC Bull. 23: 18-20.

Evans, I.D., Dutson, G.C.L. & Brooks, T.M. (1993): Cambridge Philippines Rainforest Project 1991. Final Report. Cambridge, UK.

Kemp, A.C. (1995): The Hornbills. Oxford.

Kinnaird, M.F. (1996): Indonesia's hornbill haven. Natural History 1: 40–45.

Kinnaird, M.F. & O' Brien, T.G. (1993): Preliminary observation on the breeding biology of the endemic Sulawesi Red-knobbed Hornbill (*Rhyticeros cassidix*). Trop. Biodiversity 1: 107–112.

Kinnaird, M.F., O'Brien, T.G. & Suryadi, S. (1996): Population fluctuation in Sulawesi Red-knobbed Hornbills: Tracking figs in space and time. Auk 113: 431-440.

Klop, E. (1998): Research and conservation of the Visayan Tarictic Hornbill (*Penelopides panini panini*) on Panay, the Philippines. Unpublished report of Philippine Endemic Species Conservation Project. Utrecht.

Lastimoza, L.L. & Doll, M. (1995): Notes on the behavior of *Aceros waldeni* and *Penelopides p. panini*. In: Curio, E. (ed., 1996): Second Report, Philippine Endemic Species Conservation Project, Ruhr-Universität Bochum, Germany, App. VI.

Leighton, M. & Leighton, D.R. (1983): Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton, S. L., Whitmore, T.C. & Chadwick, A.C. (eds.): Tropical Rain Forest: Ecology and Management. Oxford.

Myers, M.S. (1998): Breeding the Writhed-billed hornbill (*Aceros leucocephalus*) at the Audubon Park and Zoological Garden. Submitted.

O'Brien, T.G., Kinnaird, M.F., Dierenfeld, E.S., Conklin-Brittain, N.L., Wrangham, R.W. & Silver, S.C. (1998): What's so special about figs? Nature 392: 668.

Poonswad, P. & Kemp, A.C. (1993): Manual to the conservation of Asian Hornbills. Mahidol University, Bangkok.

Tsuji, A. (1996): Hornbills: Masters of tropical forests. Bangkok.

Witmer, M.C. (1993): Cooperative breeding by Rufous Hornbills on Mindanao Island, Philippines. Auk 110: 933-936.

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Appendix/Anhang

Food plant species fed at three nests of Writhed-billed Hornbill on Panay in 1995, 1996 (same tree, Hamtang) and 1997 (Sibaliw). Identification of plants by A. Hamann (pers. comm.).
Nahrungspflanzen, wie an drei Nestern des Runzelhornvogels auf Panay 1995, 1996 (dieselbe Höhle, Hamtang) und 1997 (Sibaliw) beobachtet. Artbestimmung durch A. Hamann (pers. Mitt.).

Scientific name	Family	Local name	Year
Ficus subcordata	Moraceae	Anino (= Nino)	'95
Ficus congesta	Moraceae	Tabuyug	'95
Ficus sp. (≥ 2 sp., incl. *F. benjamina*)	Moraceae	Dalakit	'95, '96
Ficus sp. I	Moraceae	Bantugan	'95
Ficus sp. II	Moraceae	Biri	'95
Aglaia sp. I[1]	Meliaceae	Bukabuka[2]	'95, '96
Aglaia sp. II[1]	Meliaceae	Kansulud	'95
Platea excelsa	Icainaceae	Bakán	'95
Platea sp.	Icainaceae	?	'95
Syzygium sp.	Myrtaceae	Maglumboy	'95, '97
Myristica ceylanica[3]	Myristicaceae[3]	Duguay	'97
?	?	Tisa-amo	'97
?	?	Batakulen	'97
?	?	?	'97

[1] *Aglaia* sp. III (= Babagnun) was eaten after the breeding season (Curio et al. 1996).
[2] The same name denotes possibly a species of Pterocarpaceae that also serves as nestling food.
[3] By way of comparison with the Negros name 'Duguan'.