Ökol. Vögel (Ecol. Birds) 21, 1999: 389-404

Diet composition and food provisioning of the Visayan Tarictic Hornbill (*Penelopides panini panini*) during the breeding season*

Erik Klop, Thorsten Hahn, Marion Kauth, Sophia Engel, Lucia L. Lastimoza and **Eberhard Curio****

Diet composition and food provisioning of the Visayan Tarictic Hornbill (*Penelopides panini panini*) during the breeding season. – Two nests of the Visayan Tarictic hornbill (*Penelopides panini panini*) on the Philippine island of Panay were monitored for a total of 465 hours, to reveal the diet composition both during the breeding season and in the course of the day.. About 32 different fruit species were observed to be delivered by the male Tarictic during the nestling period, which comprise about 83% of the food items. A further 16 species were found beneath the nest tree or collected from faecal samples. The main families in the diet are Moraceae (figs), Myristicaceae (nutmegs), and Palmae (palm fruits), although compared to other hornbill species the percentage figs in the diet is rather low. Red fruits are consumed most, followed by black, orange and other colours. For unknown reasons, four species of fruits have been delivered to the nest that are devoid of digestable pulp. They might serve as grit to free other seeds from digestable pulp. Small insects like flies, ants and termites make up the biggest part of the invertebrate prey, whereas the vertebrate prey consisted mainly of lizards. A distinct pattern is visible for the feeding rates of fruits and animals. Fruits are delivered especially in early morning, while animals are delivered uniformly over the day. This pattern is likely to reflect differences in the temporal and spatial availability of fruits and animal prey.

Key words: hornbill, frugivory, feeding rate, food provisioning, low-elevation forest, Philippines.

* This paper is publication No. 17 of the Philippine Endemic Species Conservation Project (PESCP) of the Frankfurt Zoological Society.

**Address for correspondence: Prof. Dr. E. Curio, Conservation Biology Unit, Faculty of Biology, Ruhr-Universität Bochum, D-44780 Bochum, Germany.

Introduction

Hornbills are among the primary frugivores in Old-world rain forests (KINNAIRD 1998). During the breeding season alone, at least 30-35 fruit species are exploited by several Asian hornbill species (KEMP 1995; KINNAIRD & O'BRIEN 1993; O'BRIEN 1997; POONSWAD et al. 1987). Male hornbills can travel more than one kilometer between nest visits, thus dispersing seeds at distances of at least 500 m from the parent plant (KINNAIRD 1998). By dispersal away from the parent, seeds may escape from predation by density responsive seed predators (JANZEN 1970) or avoid competition with the parent plant (STILES & WHITE 1986). The importance of hornbills in seed dispersal is shown by e.g. BECKER & WONG (1985), who observed that seeds of an *Aglaia* sp. (Meliaceae) were primarily dependent on Malay black hornbills (*Anthracoceros malayanus*) for escaping high seed and seedling mortality near the parent.
Information on diet selection is obviously important for both *in situ* and *ex situ* conservation of hornbills. However, virtually nothing is known about the feeding ecology of most Philippine hornbill species. The genus *Penelopides* is represented by four (KEMP 1995) or five (SIBLEY & MONROE 1990) species in the Philippines, and an additional species on the Indonesian island of Sulawesi. The medium-sized Visayan Tarictic and the sympatric Writhed-billed hornbill (*Aceros waldeni*) are the only hornbill species of the West-Visayan islands, and are both gravely endangered by hunting and habitat destruction (KLOP et al. 2000, in press). In 1996 and 1997, extensive observations were made of two Tarictic nest holes on Panay Island by members of the Philippine Endemic Species Conservation Project (PESCP), to acquire more information about the feeding ecology. This paper presents information on the diet composition and feeding frequency during the breeding season.

Methods

One Tarictic nest each in the forests of Hamtang (Valderama area) and Sibaliw (Municipality of Buruanga) was monitored for a total of 465.08 hours. Observations were made from blinds, using Leitz Televid 20-60 x 77 spotting scopes. Continuous recording (see MARTIN & BATESON 1993) was used to list time of feeding, the number and type of food items, and behaviour. Regurgitated seeds and fruits dropped by the male when feeding the female were collected for identification. Local people helped with the identification by giving the Kinaray-a names of the fruits. Later identification at the species level took place in the Philippine National Museum where all the plant samples collected are deposited.

Hamtang observations

In 1996 one nest hole was monitored during 24 days between 7 and 30 April 1996 in Hamtang Forest (11°8'N, 122°11'E) by M.K., T.H. and S.E. Hamtang is a mid-montane primary rain forest located at an elevation of around 950 m a.s.l. on the southern flanks of Mt Balabag, Panay Mountain Range. The area is relatively inaccessible because of the steepness of the slopes and the dense vegetation. However, some disturbance occurs from rattan collectors and local hunters. The nest was situated about 12 m high in a dead tree with an occupied nest hole of Blue-crowned Racquet-tails (*Prioniturus discurus*) right below it. Observations each day lasted four hours, in total 96 hours. The observation blind was located 25-30 m from the nest tree. Consecutive visits of the male Tarictic to the nest hole less than three minutes apart were considered one visit.

Sibaliw observations

A nest hole in the forest of Sibaliw area (11°49'N, 121°58'E) was observed by E.K. for 31 days between 23 April 1997 and 29 June 1997. Sibaliw is a virgin low-elevation forest located at 450 m a.s.l. in the North-west Panay peninsula mountain range. The nest hole was situated 9.3 m high in a 'Lamon'-tree near the forest edge. The nest was monitored on alternate days, although some gaps in the schedule occurred because of typhoons. In total just over 369 hours were covered. Observations started before sunrise (about 5.15) and ended at sunset (about 18.15), so that the first and the last feeding were recorded. The observations were made from a blind located 50-60 m from the nest tree. Walking between the camp site and the blind was done in the dark to avoid disturbance of the Tarictics. Each time the male Tarictic flew to the nest hole was counted as one visit, regardless of the time between consecutive visits. Six days covered less than 13 hours. For these days, the number of food deliveries had to be extrapolated to 13 hours per day, in order to allow comparison with the rest of the observation period. For analysis the data have been split up into the pre-hatching period, the nestling period, and the post-fledging period. The pre-hatching period is defined here as the period between the sealing in of the adult female and the hatching of the first egg (date unknown - 30 April), thus including a pre-laying period of unknown length. The nestling period is the period between the hatching of the first egg and the fledging of the adult female together with the first nestling (1 May - 23 June). The post-fledging period is defined here as the period between the fledging of the adult female and the fledging of the last nestling (25 June - 29 June).

Feeding rate

In order to find out whether the feeding visits and the food items delivered to the brood were equally distributed over the day, the days during the nestling period (n=23) were divided into six time periods of 130 min each. This duration was chosen arbitrarily. For each time period the number of feeding visits and the number of fruits or

animals, respectively, was calculated. The distribution of individual fruit or animal species was calculated as well; here the percentage of each species in the total number of fruits or animals per time-period was considered. A Friedman repeated-measures ANOVA was employed to detect potentially significant differences in numbers between the six time periods. This test was calculated in a procedure described by CONOVER (1980), approximating the F distribution rather than the usual chi-square distribution for reasons described by IMAN & DAVENPORT (1980). The resulting statistic is hereafter referred to as F_F, followed by the degrees of freedom written lowercase. Where appropriate, i.e. where the distribution of these periods across the day is found to be non-equal, individual periods were compared using a multiple-comparison test for related samples (see CONOVER 1980, p. 300). All these calculations are based on numbers, no conclusions can be made about the volume or weight of the food mass.

Results

Feeding behaviour

Visayan Tarictics fly at first light (between 5.15-5.30) to fruiting trees for feeding (LASTIMOZA & DOLL 1995, unpubl. manuscript). During the nestling period, the time of first food delivery was almost invariably at around 5.30 in the morning (earliest time of feeding recorded was 5.25). During the pre-hatching period and post-fledging period no feeding visits were recorded before 6.00. Although the latest time of feeding recorded was at 18.15, food deliveries later than 18.00 were exceptional. The male Tarictic used to sit on a branch opposite the nest hole before flying to it for food delivery. Begging calls emitted by the brood could be heard by LASTIMOZA & DOLL (1995, unpubl. manuscript) during observations in Hamtang. In Sibaliw the observation blind was probably too far away to hear any soft contact calls. The adult male used to regurgitate the first food item before flying to the nest hole, thus then carrying this item in the tip of its bill. Small fruits such as *Ficus heteropleura* and *Pinanga insignis* used to be regurgitated several at a time, often resulting in fruits dropping from the male's bill. Contrary to what is reported by O'BRIEN (1997), food items were not necessarily presented one at a time. The male Tarictic often presented a beak full of small fruits, which correspondingly were taken several at once by the female. Larger fruits such as *Myristica philippinensis* and *Chisocheton cumingiana* could only be regurgitated one at a time. Some smaller fruits used to be delivered in large numbers per visit, notably *Myristica glomerata* (up to 57 per visit), *Pinanga insignis* (up to 50), and small fig species such as *Ficus benjamina/heteropleura* (up to 54). This means that the Tarictic can carry loads in its crop of 60-80 grams, which is about 12-16% of its estimated body weight (see KEMP 1995).

Large insects with long legs such as stick insects or grasshoppers often caused difficulties in regurgitating. In these cases, the male used to fly back to the branch opposite the nest tree to regurgitate the food item, and then returned to the nest hole again. After feeding the male occasionally looked into the nest hole, which could last from seconds to a few minutes. This behaviour occurred more frequently later in the breeding season. Droppings on the edge of the protruding bark around the entrance used to be removed by the male before flying away. The adult female did not help in delivering food to the remaining nestling after her breaking free.

Diet composition and food provisioning

The food composition during the breeding season is given in Table 1. Data on the pre-hatching period are from observations in HAMTANG 1996 and SIBALIW 1997; the data on the nestling period and the post-fledging period are from SIBALIW 1997. The observations in Hamtang revealed a diet composition of 83.0% fruits, 12.6% animal prey, and 4.4% unidentified items during the pre-hatching period. The animal prey consisted mainly of insects, but also three eggs (of which one was identified to be of a Coleto [*Sarcops calvus*]) and one fish were delivered. In total 564 food items were delivered during 55 visits.

Table 1: Overview of the diet composition and feeding rates per period and location

	Pre-hatching period (Hamtang 1996)	Pre-hatching period (Sibaliw 1997)	Nestling period (Sibaliw 1997) (Sibaliw 1997)	Post-fledging period
Fruits	83.0%	95.8%	82.8%	95.7%
Vertebrates	0.7%	0.0%	1.0%	0.0%
Invertebrates	11.9%	2.1%	12.7%	0.0%
Unidentified	4.4%	2.1%	3.4%	4.3%
Total no. of food items	564	190	4795	46
Mean no. of visits per day ± SD	-	6.5 ± 2.14 (n=5)	23.6 ± 4.57 (n=23)	9.2 ± 9.4 (n=2)
Mean no. of food items per visit ± SD	10.3	7.6 ± 9.05 (n=25)	8.8 ± 9.62 (n=543)	5.75 ± 3.99 (n=8)
Mean no. of food items per day ± SD	-	-	208.5 ± 99.8 (n=23)	-

These data do not contain five visits during the nestling period in which an unknown number of fruits was delivered. The number of visits from observations covering less than 13 hours has been extrapolated. Only successful visits (i.e. visits with food delivery) are considered.

Table 2a: Fruits delivered by the male Tarictic during the nestling period in Sibaliw 1997.

Local name	Scientific name	Family	Number	Percent
Fruit species delivered during nestling period:				
Salauag	*Pinanga insignis* Becc.	Palmae	800	20.1%
Duguay small	*Myristica glomerata*	Myristicaceae	663	16.7%
Lunok*	*Ficus botryocarpa* Miq.	Moraceae	662	16.7%
	Ficus chrysolepis Miq.	Moraceae		
	Ficus heteropoda Miq.	Moraceae		
	Ficus pseudopalma Blanco	Moraceae		
	Ficus sp.	Moraceae		
Dalakit	*Ficus benjamina* L.	Moraceae	240	6.0%
	Ficus heteropleura Bl.	Moraceae		
Duguay	*Myristica philippinensis* Lam.	Myristicaceae	239	6.0%
Bulog	*Azidaracha indica* Merr.	Meliaceae	183	4.6%
Banilad	*Sterculia philippinensis* Merr.	Sterculiaceae	141	3.6%
Tisa-amo	*Chisocheton cumingiana* (C.DC.)Harm.	Meliaceae	109	2.7%
Maglumboy	*Syzygium densinervium* Merr.	Myrtaceae	88	2.2%
Kolintangan	–	Meliaceae	70	1.8%
Kalankang	*Alangium longiflorum* Merr.	Alangiaceae	65	1.6%
Other fruit species delivered during nestling period:			259	6.5%
Nato	*Palaquium luzoniense* (F. Vill.) Vid.	Sapotaceae		
Salumbaya	*Syzygium cumingii* L.	Myrtaceae		
Badlan	*Ficus nota* (Blco.) Merr.	Moraceae		
Alumasiga	*Agathis philippinensis* Warb.	Araucariaceae		
Maria-maria	–	–		
Sanowak	–	–		
Buguhansol	*Prunus fragrans* (Elm.) Kalkm.	Rosaceae		
Tul-ay	*Leea manillensis* Walp.	Leeaceae		
Magopinang	*Euphoria didyma* Blanco	Sapindaceae		
Balintoo	–	–		
Bakan	*Platea excelsa*	Icacinaceae		
Magupanga	*Horsfieldia megacarpa* Merr.	Myristicaceae		
Palad	*Weinmania hutchinsonii* Merr.	Cunoniaceae		
Igmin	–	–		
Lawaan	*Shorea guiso* Merr.	Dipterocarpaceae		
Manyabas	*Syzygium alvarezii* (C.B. Rod.) Merr.	Myrtaceae		
Unidentified			*453*	*11.4%*
Total			**3972**	**99.9%**

* The Kinaray-a names 'Lunok' and 'Dalakit' refer to a complex of several *Ficus*-species, and may comprise more species than the five and two species, respectively, that are listed in the table. The corresponding percentages are for both the entire Lunok-complex and Dalakit-complex.

During the observations in SIBALIW a total of 5031 food items was delivered by the male Tarictic. This is excluding five visits of which the number and type of food items could not be seen. In the pre-hatching period a total of 190 food items was recorded, consisting of 182 fruits (95.8%), 4 invertebrates (2.1%) and 4 unidentified items (2.1%). Twentyfive visits were recorded, meaning an average of 7.6 items per visit. Including extrapolated data, the mean number of visits per day was 6.5. During the nestling period an amount of 3972 fruits (82.8%) was delivered to the brood, comprising at least 32 different species representing 16 different families (see Table 2a). A further 16 species were found below the nest hole, delivered outside the nestling period, or found in feces and sealing material (see Table 2b). Fig species (Moraceae) and nutmeg species (Myristicaceae) account for almost half of the diet during this period. The families Palmae and Meliaceae account for about 20% and 10%, respectively. Of these 32 species, 12 were classified as red, 9 as (purple-)black, 3 as orange, and 8 as other colours or unknown.

Table 2b: Fruit species delivered outside the nestling period, found below the nest hole, in feces, or in sealing material (Sibaliw 1997)

Local name	Scientific name	Family
Fruit species delivered outside the nestling period:		
Malig-ang	*Shorea* sp.?	Dipterocarpaceae
Pele	*Tinomiscium philippinensis* Diels.	Menispermaceae
Fruit species found below nest but never recorded feeding:		
Badlan?	*Radermachia pinnata* (Blco.) Seem.	Bignoniaceae
Batikulen	*Areca catechu* L.	Palmae
Bere	*Ficus ulmifolia* Lam.	Moraceae
Binlud	-	-
Bugo	-	-
Bulog?	*Lithocarpus sulitii* Merr.	Fagaceae
Katilog	*Ligustrum pubinerve* Bl.	Oleaceae
Soon-manok	*Euonymus javanicus* Bl.	Celastraceae
Tabaw	*Aglaia* sp.	Meliaceae
Taglaway	*Phaeanthus ebracteolatus* (Presl.) Merr.	Annonaceae
Uya-oy	*Planchonia spectabilis* Merr.	Lecythidaceae
-	*Myristica cumingii* Warb.	Myristicaceae
Fruit species found in Tarictic feces:		
-	*Canarium* sp.	Burseraceae
Fruit species found in sealing material:		
-	*Poikilospermum suaveolens* (Bl.) Merr.	Urticaceae

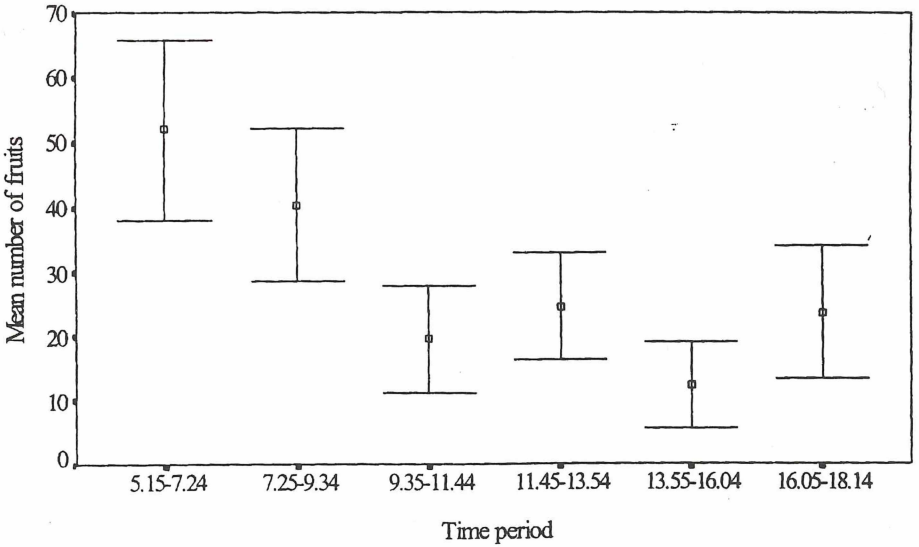

Figure 1. The distribution of fruits over the day during the nestling period. Error bars show 95% confidence interval around the mean. For statistical evaluation see text.

Delivery of fruits proved to be non-equally distributed over the day ($F_{F5,110} = 11.86$; $p < 0.05$). The feeding pattern of fruits (in numbers) is shown in Fig. 1. Fruit delivery was highest between 5.15-7.24 a.m., but the difference with period 7.25-9.34 a.m. is not significant [1]. During the first two periods significantly more fruits were delivered than in each of the other periods. Between 11.45 a.m.-13.54 p.m. and 16.05-18.14 p.m. fruit delivery was significantly higher than between 13.55-16.04 p.m.
A similar pattern is visible in the number of feeding visits in which solely fruits were delivered ($F_{F5,110} = 26.45$; $p < 0.05$). Feeding patterns over the day can also be observed for some individual fruit species. The lipid-rich *Myristica philippinensis*, a nutmeg species, was fed significantly more often in the first period than during the rest of the day, with lowest delivery rates between 9.35 a.m.-16.04 p.m. ($F_{F5,110} = 11.21$; $p < 0.05$). Roughly the same pattern can be observed for *Myristica glomerata* ($F_{F5,110} = 3.07$; $p < 0.05$) and *Chisocheton cumingiana* ($F_{F5,110} = 3.24$; $p < 0.05$). Delivery of *Azidaracha indica* was almost exclusively between 11.45 a.m.-18.14 p.m. ($F_{F5,110} = 3.32$; $p < 0.05$). All other fruit species do not show significant differences between the different time periods.

[1] Rates of fruit delivery between time periods whose rank sums are more than 20.6 apart are considered significantly different (see the multiple comparison test presented by Conover, 1980, p. 300).

Table 3: Animal prey delivered by the male Tarictic during the nestling period in Sibaliw 1997

Species	Number	Percent
Invertebrates:		
Small insects	301	49.4%
Beetles (Coleoptera)	172	28.3%
Stick insects (Phasmida)	51	8.4%
Grasshoppers (Orthoptera)	36	5.9%
Crabs (Decapoda)	18	3.0%
Cicadas (Homoptera)	11	1.8%
Insect larvae	7	1.2%
Other invertebrates delivered during nestling period:	13	2.1%
Caterpillars		
Shelled snails		
Dragonflies (Odonata)		
Spiders		
Shrimps		
Total	609	100.1%
Vertebrates:		
Lizards	36	72%
Frogs	8	16%
Fishes	3	6%
Unidentified	3	6%
Total	50	100%

Animal prey in the diet consisted of 609 invertebrates (12.7%) and 50 vertebrates (1.0%) (Table 3). About one half of the invertebrate prey consists of small insects such as flies, ants, termites and others. Various species of beetles (Coleoptera) make up just over one quarter, whereas stick insects (Phasmida), grasshoppers (Orthoptera) and other invertebrates fill up the remaining part.

No significant differences between the different time periods over the day were found in the delivery of animal prey ($F_{F5,110} = 1.68$; p = n.s.). Fig. 2 shows the feeding pattern of animal prey (vertebrate and invertebrate) over the day. Visits in which solely animals were delivered were also equally distributed over the day ($F_{F5,110} = 1.29$; p = n.s.).

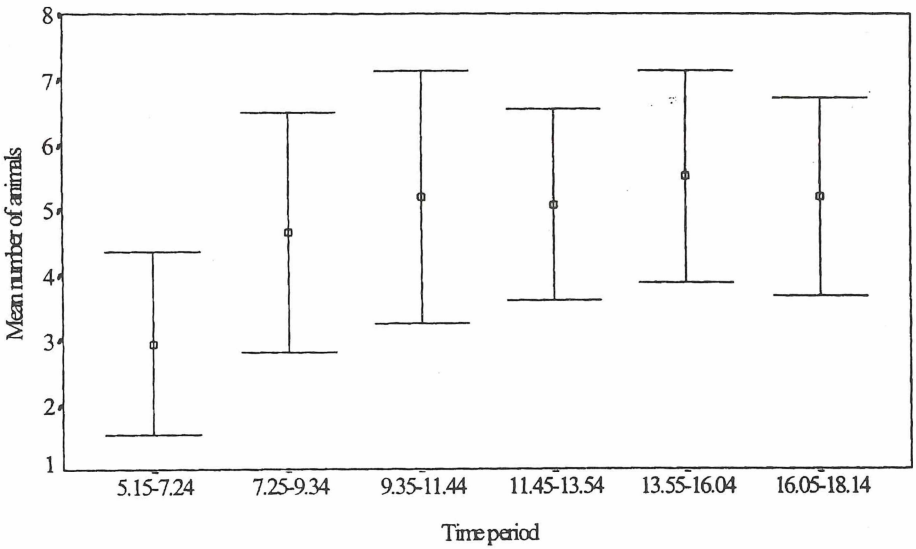

Figure 2. The distribution of animal prey over the day during the nestling period. Error bars show 95% confidence interval around the mean. For statistical evaluation see text.

A remaining 164 items (3.4%) could not be identified. The total of 4795 food items was spread over 543 visits, thus corresponding to a mean number of 8.8 items per visit. The mean number of feeding visits per day was 23.6.

In the two days of the post-fledging period 46 food items were recorded, of which 44 (95.7%) were fruits and 2 unidentified (4.3%). The mean number of items per visit was 5.75; the mean number of visits per day was 9.2.

Feeding visits differed greatly in composition of delivered food items. In 251 out of 605 recorded feeding visits during the complete observation period, solely fruits were delivered. 147 visits contained both fruits and animals, while 119 visits contained only animal prey. The remaining 59 visits contained only unidentified items. In 29 visits no food was delivered, seven of which occurred in the post-fledging period.

Conclusion and Discussion

Diet composition

Fruits make up the main part of the diet, though with 14% animals during the nestling period the Visayan Tarictic proved to be more carnivorous than the sympatric Writhed-billed Hornbill (see KAUTH et al. 1998). At least 48 different fruit species representing 25 families are exploited by the Visayan Tarictic during the breeding season. The main families are Moraceae (figs), Myristicaceae (nutmegs), and Palmae (palm fruits), to which two-thirds of the delivered fruit species belong. As has been reported previously for other hornbill species, fig species are important as a basic food resource. Figs are an excellent source of sugars, proteins, calcium, and moisture, have a high pulp to seed ratio, and are available year-round (KEMP 1995; KINNAIRD et al. 1996; O'BRIEN et al. 1998). However, compared to the diet of other frugivorous hornbill species, the percentage of figs in the diet of the Visayan Tarictic is relatively low (about 23%). In the breeding season diet of the North Sulawesi Tarictic, figs accounted for one-third of the fruits delivered (O'BRIEN 1997). GONZALES & DANS (1996, unpubl. report) observed the Polillo Tarictic (*Penelopides manillae subnigra*) to forage mainly on *Ficus caudatifolia* and *Ficus benjamina*. A low proportion of figs in the diet of the Visayan Tarictic may reflect either a low density of figs in the study area, or a preference for other fruit species. Since the syntopic Writhed-billed Hornbill feeds its family with 33% figs during the breeding season (KAUTH et al. 1998), a corresponding shortage of figs can be ruled out. The high proportion of nutmeg species (Myristicaceae) in the diet of the Tarictic parallels previous observations that fruits with dehiscent capsules and fleshy, oily arils around the seed are highly attractive to hornbills (GAUTIER-HION et al. 1985; KEMP 1995). Clearly shown by the observations is a high consumption of red fruits, followed by (purple-)black and orange. The attractiveness of red and purple-black fruits to hornbills or birds in general is well documented (e.g. BREITWISCH 1983; GAUTIER-HION et al., 1985; KEMP 1995; SURYADI et al. 1994), and although the precise order of preference depends on the species and habitat, the choice of these colours seems universal and correlates with the hornbills' good discrimination of red wavelengths (GAUTIER-HION et al. 1985).

A number of fruit species are delivered both within (Table 2a) and outside the nestling period (Table 2b) that are devoid of digestable pulp or are wind-dispersed. Among the former species are the common dipterocarps (*Shorea guiso, Shorea* sp.) and *Lithocarpus sulitii*, among the latter *Agathis philippinensis*. One might speculate that by virtue of their hardness these species are utilized as kind of grit to help detach the pulp from the bulk of the fruits utilized. An even longer list of edible species that have been found below the nest have never been observed being fed to the brood inside (Table 2b). Perhaps they have been fed so rarely that by pure chance they had been fed on the alternate days without observation.

The male seemed to be opportunistic in the hunting for animal prey, which was often collected in the close proximity of the nest tree. Besides terrestrial prey, both the Hamtang and Sibaliw male hunted along river streams for fish, crabs, shrimps, and small crayfish. The delivery of a Coleto (*Sarcops calvus*) egg by the Hamtang male evinces predation of tree cavities, a behaviour also observed in other hornbill species (e.g. *Buceros bicornis*, KANNAN & JAMES 1997). The proportion of animal prey in the diet during the pre-hatching period is considerably higher for the Hamtang-pair than for the Sibaliw-pair. Vertebrates accounted for only a small part of the animal prey, and were only delivered during the nestling period. During the entire breeding period of the North Sulawesi Tarictic, the amount of invertebrate prey varied between 7% and 26% (O'BRIEN 1997). The only vertebrate prey that was observed to be delivered to the nest, was an unidentified bat species (O'BRIEN 1997). The Writhed-billed hornbill includes a noticeably smaller amount of animal food in its diet than the Visayan Tarictic (see KAUTH et al. 1998), demonstrating a higher appetence for it by the Tarictic or a lower hunting ability of the Writhed-bill.

Daily distribution of provisioning

Food delivery by the male Tarictic occurs throughout the entire day, but during the nestling period the male starts earlier than when the female is still incubating. During early morning (5.15-9.34) feeding rates are highest, falling to a minimum at mid-afternoon, and increasing again towards late afternoon. This pattern is largely governed by the feeding of fruits, which accounts for 85% of the sample units. A peak in fruit consumption in the early morning may reflect the high accessibility or availability of fruits before they are depleted by other frugivores. Since part of the fruit trees are patchily dispersed throughout the habitat (STILES & WHITE 1986), it is likely that early and frequent visits to nearby trees reduce the necessity of foraging later in the day over a larger area to obtain an equal amount of food. The lipid-rich *Myristica philippinensis*, *M. glomerata* and *Chisocheton cumingiana* were fed especially during early morning, while other fruit species were (as a proportion of the fruit numbers per time-period) spread evenly over the day. A similar pattern was reported by HOWE (1977) for the arillate seeds of the Costa Rican *Casearia corymbosa* (Flacourtiaceae) which dehisce during the night. Feeding rates of toucans (Ramphastidae) were high early in the morning, but decreased markedly by late morning due to depletion of the fruits rather than loss of interest (HOWE 1977; HOWE & ESTABROOK 1977). BECKER & WONG (1985) observed that Malay Black hornbills (*Anthracoceros malayanus*) tended to visit meliaceous crowns early in the morning, especially near dawn, before squirrels could predate on many seeds. They predicted that capsules dehisce after dusk so that the seeds are available to the hornbills in the early morning (BECKER & WONG 1985).

In contrast to fruits, animal prey is delivered uniformly throughout the day. Between 5.15-7.24 feeding rates for animals are markedly lower than during the rest of the day, but this difference is not statistically significant. This uniform pattern might be caused

by the availability of animal prey. Since the Tarictic seems to hunt for animal prey mainly in its own territory, depletion of these food sources by other Tarictics is not likely to occur. The absence of competitors, or the plentiness of animal food, probably avoids the need of 'being the first one at the food source'.
During the nestling period feeding rates are obviously higher than when the female is still incubating, according to the demand of food by the brood. The higher number of food items per visit for the Hamtang observations is probably caused by a different method of counting the visits (see methods). Some fruits look nearly identical in a certain stage of fruiting and may sometimes have been confused, especially when the view was limited because of darkness or heavy rain. However, during the observation period the observers became more and more familiar with the different fruits, thus reducing the chance of confusion.

Seed dispersal
The extent to which the Tarictic is an effective seed disperser needs further research. As is shown in this study, a large number of fruit species is consumed, some of which appear to be primarily dependent on hornbill dispersal because of large fruit or seed size (e.g. *Myristica philippinensis, Chisocheton cumingiana*). Since most seeds that are voided by the birds will accumulate beneath the nest hole, fruits adapted to clumped dispersal (see HOWE 1989) are most likely to survive. Outside the breeding season hornbills disperse seeds in a more scattered way (WHITNEY et al. 1998), thus supporting fruits adapted to scatter-dispersal (see HOWE 1989). As pointed out by WHITNEY et al. (1998), it would be interesting to see whether there are any differences in fruit selection in- and outside the breeding season based on these theoretical grounds. Although the observations itself were extensive, the number of nests monitored is small (2), which makes generalisation of the results difficult. In particular the diet during the pre-hatching period and post-fledging period is based on relatively few data, and especially the invertebrate proportion varies widely between both nests (see Table 1). Many factors influence fruit selection by birds, such as colour, pulp to seed ratio, ripeness, palatability and nutrient contents, accessibility, crop size, spacing between fruit clumps, and local fruit abundance (see GAUTIER-HION et al. 1985; MOERMOND et al. 1986). The importance of each of these factors for the fruit choice of the Visayan Tarictic, however, is unknown. Analysis of the nutritional value of the various food items, as well as measurements or estimations of the volume and weight of the food mass, is needed to get more insight into the nutritional requirements of the Tarictic and its brood during the breeding season. It should be realised that the diet as described may not only reflect preferences for particular fruit species, but also the spatial distributions of those fruits and their proximity to alternative fruit choices (DENSLOW et al. 1986). Instead of travelling to preferred fruit trees further away, frugivores may choose to consume lower quality fruits growing in the vicinity (DENSLOW et al. 1986; STILES & WHITE 1986).

Zusammenfassung

Nahrungszusammensetzung und Fütterverhalten des Visayas-Tariktikhornvogel (*Penelopides panini panini*) während der Brutzeit

Um das spärliche Wissen über die Ernährung philippinischer Hornvögel zu erweitern, wurden erstmals zwei Bruten des Visayas-Tariktiks (*Penelopides panini panini*) auf Panay insgesamt 465 Stunden beobachtet. Hierbei ergab sich die Verteilung der vom Männchen übergebenen Nahrung im Verlauf der Brutsaison sowie im Tagesablauf. Etwa 32 Fruchtarten, die ca. 83 % aller Nahrungsbrocken ausmachen, wurden während der Nestlingszeit verfüttert. Weitere 16 Arten fanden sich als Nahrungsreste unter dem Höhlenbaum oder im Kot. Die überwiegend genutzten Familien waren Feigen (Moraceae), die Muskatnußbäume (Myristicaceae) und die Palmen (Palmae), obwohl Feigen im Vergleich zu anderen Hornvogelarten ziemlich zurücktraten. Unter den genutzten Früchten herrschte Rot vor, gefolgt von Orange, Schwarz und anderen Farben. Aus unbekanntem Grund enthielt der Speisezettel vier Fruchtarten ohne verdaubares Fruchtfleisch; sie mögen als "Magensteine" zur mechanischen Sonderung von Samen und verdaubarem Fleisch anderer Arten wirken. Kleine Insekten wie Fliegen, Ameisen und Termiten machen die Hauptmasse der wirbellosen Beute aus, während Echsen (Skinke) unter den Wirbeltieren hervorstechen; aber es gab auch Fische und Frösche. Das Auftreten von Süßwasserfischen und -garnelen weisen den Tariktik auch als Gelegenheitsfischer aus. Die Verfütterung von Früchten und Tieren folgt einem bezeichnenden Tageslauf. Während Früchte früh am Morgen die Hauptspeise ausmachen, streut tierliche Beute gleichmäßig über den ganzen Tag. Dieses Füttermuster spiegelt wahrscheinlich Unterschiede der zeitlichen und räumlichen Verfügbarkeit von Früchten und Beutetieren wider.

Acknowledgements

Support was provided by the members of the PESCP teams in Hamtang and Sibaliw, in particular J. Arsenio, M. Arsenio, M. Ballhaus, T. Dalumpines, R. Ebon, B. Gonzales, R. Maximo, G. Meier, S. Peters, Y. de Soye, and B. Tacud. E. Barbon and E. Reynoso of the Philippine National Museum (Manila) helped decisively with the identification of plant samples. Financial support came from the Frankfurt Zoological Society, the Andreas-Stihl-Stiftung, the EU, the German Ornithologists' Society, the Ministry of Science and Research of the Land North Rhine Westfalia, Prof. Dr Dr mult. h.c. Ernst Mayr, Cambridge, Mass., and Mr. Claus Sudhoff (Cavite). The Protected Areas and Wildife Bureau of the DENR (Director Wilfrido S. Pollisco, Region VI RED R. Geollegue and RTD R. Pangahas) and West Visayas State University (President Dr. Bernabe B. Cocjin and dean of College of Agriculture and For-

estry Dr. ELEODORO L. ALICANTE) provided advice and support throughout. To all these persons and organizations we are immensely grateful.

References

BECKER, P. & M. WONG (1985): Seed Dispersal, Seed Predation, and Juvenile Mortality of *Aglaia* sp. (Meliaceae) in Lowland Dipterocarp Rainforest. Biotropica 17: 230-237. – BREITWISCH, R. (1983): Frugivores at a Fruiting *Ficus* Vine in a Southern Cameroon Tropical Wet Forest. Biotropica 15: 125-128.

CONOVER, W.J. (1980): Practical Nonparametric Statistics, second edition. John Wiley & Sons, New York.

DENSLOW, J.S., T. C. MOERMOND & D.J. LEVEY (1986): Spatial components of fruit display in understory trees and shrubs. In: ESTRADA, A. & FLEMING, T.H. (eds.), Frugivores and seed dispersal. Dr W. Junk Publishers, Dordrecht, pp. 37-44.

GAUTIER-HION, A., J. M. DUPLANTIER, R. QURIS, F. FEER, C. SOURD, J. P. DECOUX, G. DUBOST, L. EMMONS, C. ERARD, P. HECKETSWEILER, A. MOUNGAZI, C. ROUSSILHON & J.M.THIOLLAY (1985): Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia (Berlin) 65: 324-337. – GONZALES, J.C.T. & A. T. L. DANS (1996): Distribution and Ecology of the Polillo Tarictic Hornbill *Penelopides manillae subnigra*, and notes on threatened fauna in the Polillo Islands, Philippines. Unpublished Report, University of the Philippines, Los Baños.

HOWE, H.F. (1977): Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58: 539-550. – HOWE, H.F. (1989): Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79: 417-426. – HOWE, H.F. & G. F. ESTABROOK,1977. On intraspecific competition for avian dispersers in tropical trees. Am. Nat. 111: 817-832.

IMAN, R.L. & DAVENPORT, J.M. (1980). Approximations of the critical region of the Friedman statistic. Communications in Statistics A9(6)5.8.

JANZEN, D.H. (1970). Herbivores and the number of tree species in tropical forests. Am. Nat. 104: 501-528.

KANNAN, R. & D. A. JAMES (1997): Breeding biology of the Great Pied Hornbill (*Buceros bicornis*) in the Anaimalai hills of southern India. J. Bombay Nat. Hist. Soc. 94:451-465.

KAUTH, M., S. ENGEL, L. L. LASTIMOZA, & E. CURIO (1998): Observations on the breeding biology of the Writhed-billed Hornbill (*Aceros waldeni*) in the Philippines. J. Ornithol. 139:475-483. – KEMP, A.C. (1995): The hornbills. Oxford University Press, Oxford. – KINNAIRD, M.F. (1998): Evidence for Effective Seed Dispersal by the Sulawesi Red-Knobbed Hornbill, *Aceros cassidix*. Biotropica 30: 50-55. – KINNAIRD, M.F. & T. G. O'BRIEN (1993): Preliminary observation on the breeding biology of the endemic Sulawesi Red-knobbed Hornbill (*Rhyticeros cassidix*). Trop. Biodiversity 1: 107-112. – KINNAIRD, M.F., T. G. O'BRIEN, & S. SURYADI (1996): Population fluctuation in Sulawesi Red-knobbed Hornbills: Tracking figs in space and time. Auk 113: 431-440. – KLOP, E., E. CURIO & L. L. LASTIMOZA (2000): Breeding biology, nest site characteristics and nest spacing of the Visayan Tarictic Hornbill (*Penelopides panini panini*) on Panay, Philippines. Bird Cons. Intl. 10 (in press).

MARTIN, P. & P. BATESON (1993): Measuring behaviour: An introductory guide. Second edition, Cambridge University Press, Cambridge. – MOERMOND, T.C., J. S. DENSLOW, D. J. LEVEY & C.

E. SANTANA (1986): The influence of morphology on fruit choice in neotropical birds. In: ESTRADA, A. & FLEMING, T.H. (eds.), Frugivores and seed dispersal. Dr W. Junk Publishers, Dordrecht, pp. 137-146.
O'BRIEN, T.G. (1997). Behavioural ecology of the North Sulawesi Tarictic Hornbill *Penelopides exarhatus exarhatus* during the breeding season. Ibis 139: 97-101. – O'BRIEN, T.G., M. F. KINNAIRD, E. S. DIERENFELD, N. L. CONKLIN-BRITTAIN, R. W. WRANGHAM & S. C. SILVER (1998): What's so special about figs? Nature 392: 668.
POONSWAD, P., A.TSUJI, & C. NGAMPONGSAI (1987): A comparative study on breeding biology of sympatric hornbill species (Bucerotidae) in Thailand with implications for breeding in captivity. Proceedings Jean Delacour/IFCB Symposium on Breeding Birds in Captivity. Los Angeles, California.
SIBLEY, C.G. & B. L. MONROE (1990): Distribution and taxonomy of birds of the world. Yale University Press, New Haven and London. – STILES, E.W. & D.W. WHITE (1986): Seed deposition patterns: influence of season, nutrients, and vegetation structure. In: ESTRADA, A. & FLEMING, T.H. (eds.), Frugivores and seed dispersal. Dr W. Junk Publishers, Dordrecht, pp. 45-54. – SURYADI, S., M. F. KINNAIRD, T. G. O'BRIEN, J. SUPRIATNA & S. SOMADIKARTA (1994): Food preferences of the Sulawesi Red-Knobbed Hornbill during the breeding season. Trop. Biodiversity 2: 377-383.
WHITNEY, K.D., M. K. FOGIEL, A.M. LAMPERTI, K. M. HOLBROOK, D.J. STAUFFER, B. D. HARDESTY, V. T. PARKER & T. B. SMITH (1998): Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. J. Trop. Ecology 14: 351-371.