

RESEARCH ARTICLE

High Frequency of Leaf Swallowing and Its Relationship to Intestinal Parasite Expulsion in “Village” Chimpanzees at Bulindi, Uganda

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Self-medication by great apes to control intestinal parasite infections has been documented at sites across Africa. Chimpanzees (*Pan troglodytes*) swallow the leaves of certain plant species whole, without chewing. Previous studies demonstrated a relationship between chimpanzee leaf swallowing and expulsion of nematode worms (*Oesophagostomum* sp.) and tapeworms (*Bertiella* sp.) in dung. We investigated the relationship between leaf swallowing and parasite expulsion in chimpanzees inhabiting a fragmented forest–farm mosaic at Bulindi, Uganda. During 13 months whole undigested leaves occurred in chimpanzee dung at a considerably higher frequency (10.4% of dungs) than at other sites (0.4–4.0%). Leaf swallowing occurred year-round and showed no pronounced seasonality. Chimpanzees egested adults of multiple species of *Oesophagostomum* (including *O. stephanostomum*) and proglottids of two tapeworms—*Bertiella* sp. and probably *Raillietina* sp. The latter may not be a true infection, but the byproduct of predation on domestic fowl. Compared to previous studies, the co-occurrence of whole leaves and parasites in chimpanzee dung was low. Whereas the presence of leaves in dung increased the probability of adult nematode expulsion, no association between leaf swallowing and the shedding of tapeworm proglottids was apparent. Anthropogenic habitat changes have been linked to alterations in host–parasite interactions. At Bulindi, deforestation for agriculture has increased contact between apes and people. Elevated levels of leaf swallowing could indicate these chimpanzees are especially vulnerable to parasite infections, possibly due to environmental changes and/or increased stress levels arising from a high frequency of contact with humans. Frequent self-medication by chimpanzees in a high-risk environment could be a generalized adaptation to multiple parasite infections that respond differently to the behavior. Future parasitological surveys of apes and humans at Bulindi are needed for chimpanzee health monitoring and management, and to investigate the potential for disease transmission among apes, people, and domestic animals. *Am. J. Primatol.* 74:642–650, 2012. © 2012 Wiley Periodicals, Inc.

Key words: chimpanzee; habitat disturbance; host–parasite relationships; *Oesophagostomum*; self-medication; tapeworm

INTRODUCTION

Medicinal plant use as a means of controlling intestinal parasites has been documented in multiple populations of wild African apes [Huffman, 2001]. In particular, chimpanzees at sites across tropical Africa swallow the whole leaves of >40 different plant species without chewing [Fowler et al., 2007; Huffman, 2001; Huffman et al., 1997; Pruett & Johnson-Fulton, 2003; Wrangham, 1995; Wrangham & Nishida, 1983]. The unifying physical characteristic of the leaves is their rough, bristly surface [Huffman, 1997]. This rare behavior confers no nutritional benefit since the leaves are passed undigested in dung. At Mahale, Tanzania, a positive relationship was found between the occurrence of whole leaves and adult nematode worms (*Oesophagostomum stephanostomum*) in chimpanzee dung [Huff-

man et al., 1996]. Similarly, whole leaves and tapeworm proglottids (*Bertiella studeri*) appeared together, or separately but in the same season, in chimpanzee dung at Kibale [Wrangham, 1995] and Budongo [Huffman et al., 2009], in Uganda. In some

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instances adult *Oesophagostomum* have been found trapped between the folds of leaves or attached to the leaf surface [Fowler et al., 2007; Huffman et al., 1996].

While these observations might imply that the rough leaves dislodge parasites and cause proglottids to be shed, Huffman & Caton [2001] proposed an alternative physical mechanism by which leaf swallowing controls *Oesophagostomum* nematode infection: irritation caused by the leaves acts as a purgative, rapidly increasing gut motility and causing expulsion of adult worms, thereby disrupting the life cycle of the parasite. Repeated flushing of the gastrointestinal tract during peak infection periods (the rainy season at Mahale) may be effective in reducing overall worm burden [Huffman & Caton, 2001]. In contrast to these findings, however, leaf swallowing by chimpanzees at Budongo, Uganda, which has a less seasonal climate, was not associated with *Oesophagostomum* worm expulsion [Huffman et al., 2009]. Variation between habitats in environmental factors such as rainfall can influence infection dynamics, potentially causing differences in the health and behavior of chimpanzee hosts [Huffman et al., 2009]. In the case of cestode infection, the shedding of proglottids is a normal part of the tapeworm's reproductive strategy [Stunkard, 1940]. Consequently, the role of leaf swallowing in alleviating tapeworm infection is unclear [Huffman, 1997; Wrangham, 1995].

Studies of self-medication in apes living in disturbed environments in close contact with people are of particular interest, as they add a new dimension to the study of host-modified response to disease, and may also tell us something about the incidence of potentially zoonotic parasite infections in wild apes. Many natural habitats are undergoing extensive modifications as a result of human activities. Anthropogenic environmental changes including agricultural encroachment, logging, forest degradation, and fragmentation have been linked to alterations in host–parasite interactions, which may facilitate increased pathogen transmission between humans, primates, and domestic animals [Chapman et al., 2006; Gillespie & Chapman, 2008; Gillespie et al., 2005; Kowalewski et al., 2011; Mbora & McPeck, 2009; Vitazkova, 2009; Wenz et al., 2010; Weyher, 2009]. Great apes increasingly range within human-modified habitats such as farm–forest ecotones in proximity to people [Hockings & Humle, 2009]. Because of the close phylogenetic relationship between humans and apes, the potential for pathogen exchange between them is increased in shared landscapes [Goldberg et al., 2007; Krief et al., 2010; Leendertz et al., 2006; Rwego et al., 2008]. At Bulindi, Uganda, a community of eastern chimpanzees (*Pan troglodytes schweinfurthii*) inhabit a degraded forest–agriculture mosaic and encounter humans and domestic animals daily [McLennan &

Hill, 2010]. The feces of humans, cattle, and dogs were regularly seen in and around forest patches—a chimpanzee knuckle print was once observed in fresh human excrement—and chimpanzees often defecated in gardens and near homesteads, particularly during crop-raiding forays [McLennan, 2010a]. Given this situation, we feel that the potential for pathogen transmission between humans, chimpanzees, and domestic animals might be higher at this site than most other field sites where leaf swallowing has been previously reported.

The relationship between leaf swallowing and parasite expulsion in chimpanzees that range wholly within a human-dominated environment has not previously been examined. Therefore, the aims of this preliminary study were to: (i) determine the frequency and seasonality of whole leaf swallowing in a chimpanzee community living in exceptionally close proximity to humans; and (ii) establish the relationship between leaf swallowing and cestode and nematode expulsion.

METHODS

Study Site

Chimpanzees were studied at Bulindi, western Uganda, during 2006–2008 [McLennan, 2010b]. Bulindi (1°28'N, 31°28'E) is located in Hoima District, 25 km south of the Budongo Forest (Fig. 1). The habitat matrix within the 40 km² study area comprises a mosaic of small (<50 ha) riverine forest patches and wooded grassland encircled by cultivated and fallow fields and village areas. Human population density in the district was 95.4 individuals per km² in 2002 and the annual growth rate during 1991–2002 was 4.7% [UBOS, 2007]. Mean annual precipitation was 1,461 mm in 2001–2007. Rainfall is bimodal with wet seasons (>100 mm mean monthly rainfall) occurring in March–May and July–November. A 3-month dry season (<50 mm rainfall) occurs between December–February, and a second, transient dry season (<100 mm rainfall) is evident in June. Rainfall during 2007 deviated somewhat from this pattern, possibly due to the effects of La Niña (cf. Fig. 2).

The Bulindi chimpanzee community is one of multiple small chimpanzee groups inhabiting unprotected remnant forest patches in the heavily cultivated landscape south of Budongo [McLennan, 2008]. There were approximately 25 chimpanzees at Bulindi in 2006–2008. During that period, forest patches were extensively logged and villagers regularly entered the forest to collect water, fuel wood, poles, and other resources. Forest was also being cleared for agriculture, particularly tobacco cash cropping.

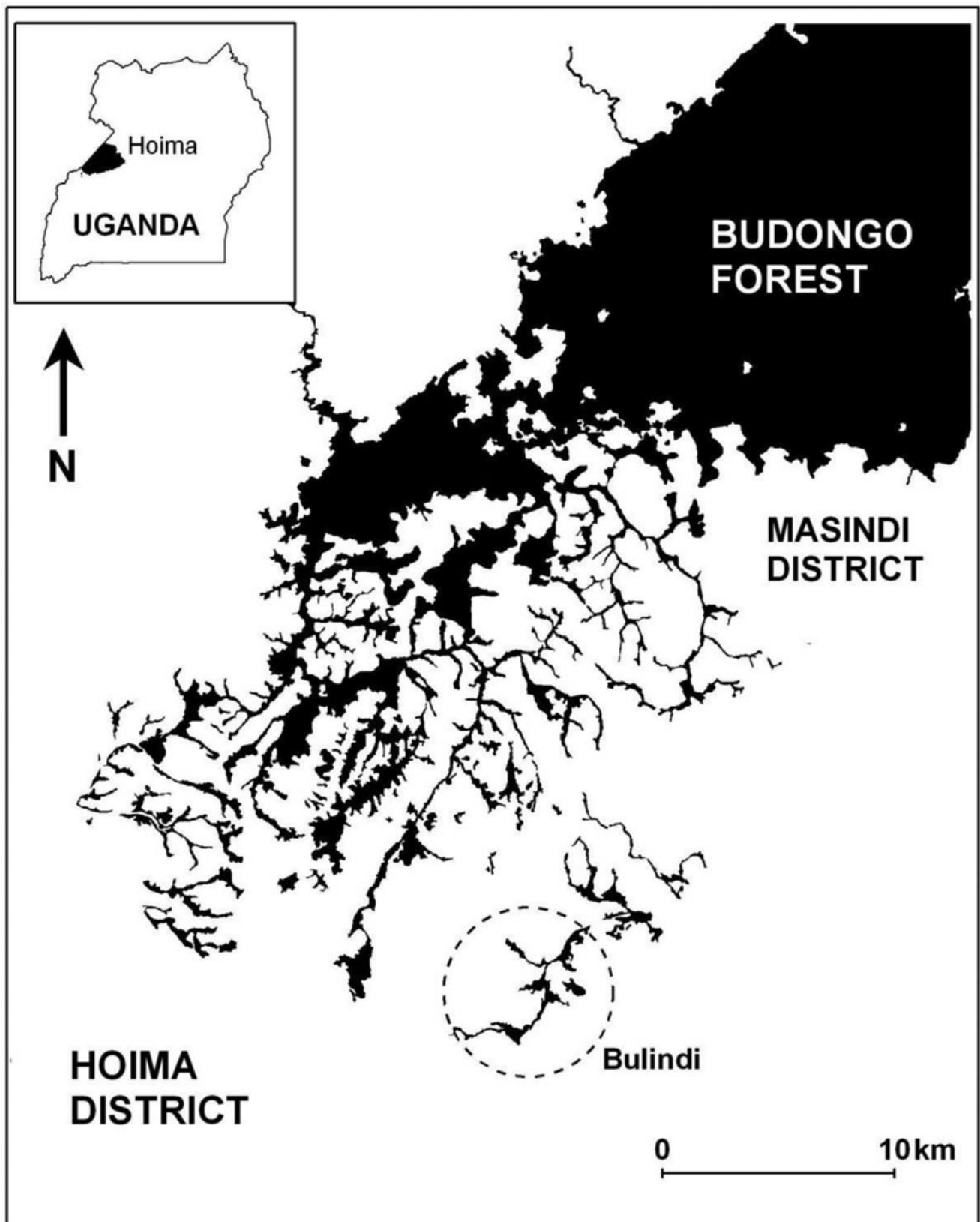


Fig. 1. Map showing the Budongo Forest in Masindi District and outlying riverine forest patches to the south. Many of the forest patches are utilized by small groups of chimpanzees [McLennan, 2008]. The study site at Bulindi in Hoima District is encircled. [Courtesy of Nadine Laporte].

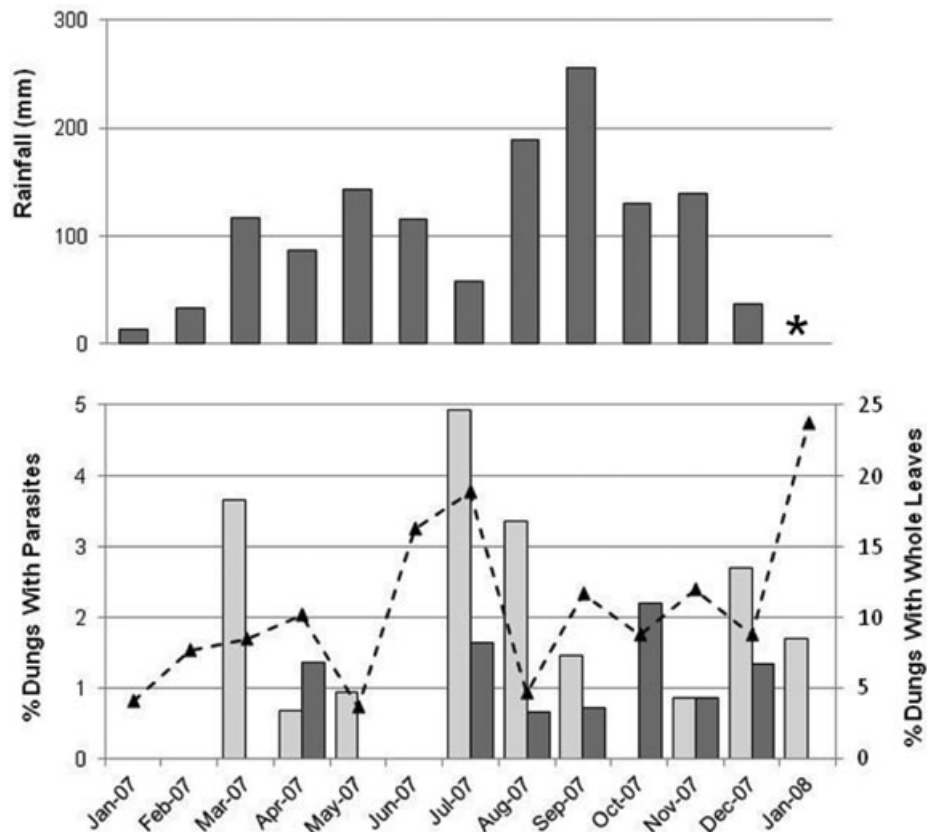


Fig. 2. Relationship between monthly rainfall and percentage of chimpanzee dungs containing whole leaves and macroscopic parasites, Jan 2007–Jan 2008. *Upper figure*: Bars depict monthly rainfall; *Rainfall data were unavailable for Jan 2008, but January is a dry month (<50 mm rainfall; 2001–2007). *Lower figure*: Dashed line shows monthly percentage of dungs containing whole leaves. Bars show monthly percentage of dungs containing parasites: tapeworm proglottids (light grey) and adult nematodes (dark grey). Dung sample size per month: Jan 07 = 49, Feb = 91, Mar = 82, Apr = 147, May = 107, Jun = 92, Jul = 122, Aug = 149, Sep = 137, Oct = 136, Nov = 117, Dec = 148, Jan 08 = 59. Note that in the month preceding the study (December 2006) one of four dungs collected opportunistically contained a proglottid; thus tapeworms were infecting the chimpanzees for a minimum of 14 months.

Data Collection

Chimpanzees at Bulindi are not habituated to close observation [McLennan & Hill, 2010]. Therefore leaf swallowing was investigated via fecal analysis. Fresh dung specimens (≤ 1 day old) were collected over 13 months between January 2007 and January 2008 ($N = 1,436$, monthly mean = 110.5, range 49–149). Dungs were collected on an average of 17 days per month (range 10–22), and the mean number of specimens collected per “dung collection day” was 6.6 (± 4.5 SD). Dungs were collected beneath night nests, on habitually used trails, and from areas recently vacated by apes. Only one specimen was collected per night nest. If successive dung piles (e.g., along trails) were judged to be from single individuals, one specimen was collected only. Dungs were stored in plastic bags, weighed (beginning June 2007), and washed through a 1-mm sieve within 3 days of collection. Whole leaves were counted and dried, and macroscopic parasites (nematode worms and tapeworm proglottids) were preserved in 70%

ethanol for identification. Parasites were identified by William Kabasa and Michael Ocaido at the Faculty of Veterinary Medicine, Makerere University, Uganda. Subsequent verification was performed by Takashi Iwaki, a specialist in primate parasitology at the Meguro Parasitological Museum, Tokyo. This research adhered to the legal requirements of Uganda and the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. The study had full ethical approval of Oxford Brookes University Research Ethics Committee.

Data Analysis

We used Pearson’s correlations to examine the relationship between monthly rainfall and the frequency of whole leaves in dungs. Spearman’s rank correlations were used to test for a relationship between monthly frequencies of whole leaves and macroscopic parasites (cestodes and nematodes) in dungs as parasite data were nonnormally

distributed. We tested if dungs containing whole leaves were more likely to also contain parasites with Fisher's exact test. The analysis was performed using SPSS version 17 and significance was set at $P < 0.05$.

RESULTS

Frequency of Whole Leaves in Dung

Leaf swallowing was not a rare occurrence at Bulindi. Whole undigested leaves were present in 149 chimpanzee dungs (10.4%), on an average of 40.4% dung collection days per month (range 15–80%). The mean monthly percentage of dungs containing whole leaves was 10.7% (± 5.9 SD, range 3.7–23.7%). This is a considerably higher frequency than reported at other sites for which comparable data are available ($\leq 4\%$ at all other sites; Table I). Leaves were usually folded 2–3 times, but sometimes occurred as very tightly folded “parcels” (folded >3 times); occasionally they appeared unfolded in dung. Rarely, only the distal half of the leaf was recovered. For weighed dungs (61% of the total sample), the wet weight of specimens with whole leaves ranged between 9–253 g (mean = 96.1 ± 49.8 SD; $N = 97$), indicating leaf swallowing was not limited to a particular age–sex class. The number of individual leaves recovered ranged from 1–49 but averaged less than 10 (mean = 6.1 ± 8.3 SD; median = 3). The mean number of leaves per 100 g (wet) dung was 7.6 (± 11.2 SD; median = 3.8).

Leaf swallowing occurred in all months and did not peak during wet months (Fig. 2). There was no correlation between monthly rainfall and proportion of dungs containing whole leaves ($r = 0.014$, $N = 12$, $P = 0.97$; January 2008 was excluded because rainfall data were unavailable). Because *Oesophagostomum* reinfection peaked 1–2 months following the onset of the rainy season at Mahale [Huffman et al., 1997], the association between monthly percentage of dungs containing leaves and monthly rainfall in

the preceding 1 and 2 months was tested, but there was no correlation ($P = 0.79$ and 0.87 , respectively). Nevertheless, leaf swallowing peaked twice during the study; first, during the transition from wet-to-transient dry season (June–July 2007), and again in January 2008, at the height of the main dry season (Fig. 2).

Chimpanzees swallowed leaves of five species of shrub or herb and at least one species of grass (Table II). All leaves were scabrous, bristly, or velvety. The most commonly swallowed leaves were *Aneilema nyanense* (Commelinaceae), occurring in 82% of cases ($N = 122$) and seen in dung in all months. Two other species occurred occasionally in dung. *Desmodium velutinum* (Fabaceae) leaves occurred in 10% of cases, mostly during June–July. Leaves of the invasive weed *Lantana camara* (Verbenaceae) were swallowed during September–December only (8% of cases). Another two species (*Acalypha* sp. and ?*Erythrocca* sp.) were each found once in dung. Unidentified hispid grass blades were present three times in dung (Table II).

Parasite Prevalence

Two different cestodes and at least two species of adult nematode were expelled in dung. Tapeworm proglottids included *Bertiella* sp. and others of a different genus, probably *Raillietina*. All identified nematodes were *Oesophagostomum* spp. (including *O. stephanostomum* and ≥ 1 unidentified species). The overall frequency of all macroscopic parasites in dung was 2.4%. Because not all egested proglottids were identified, they were simply grouped as tapeworms. Tapeworms occurred in 1.7% of dungs ($N = 24$; in 9/13 months), whereas adult *Oesophagostomum* occurred in 0.8% ($N = 12$; 7/13 months). One dung specimen collected at a homestead, after male chimpanzees had interacted aggressively with their reflections in the glass door of the house [McLennan, 2010a], contained two *Bertiella*

TABLE I. Frequency (Percentage of Dungs) Containing Whole, Undigested Leaves at Different Chimpanzee Study Sites. Frequency is Shown as the Overall Percentage of Dungs Containing Leaves (O) and/or the Mean Monthly Percentage of Dungs with Leaves (M)

Site	Country	Percentage of dungs with whole leaves	Number of dung specimens inspected	Duration of study	Reference
Mahale	Tanzania	2.8% (M)	2,309	1975–1979	Wrangham & Nishida [1983]
Gombe	Tanzania	3.1% (M)	1,946	1964–1967	Wrangham & Goodall [1989]
Kibale (Kanyawara)	Uganda	2.5% (O), 1.5% (M)	1,696	78 months	Wrangham [1995]
Kibale (Ngogo)	Uganda	0.4% (O), 0.9% (M)	1,198	73 months	Wrangham [1995]
Kahuzi-Biega	DRC	2.2% (O)	7,212	78 months	Basabose [2002]
Budongo	Uganda	0.7% (O)	299	9 months	Pebsworth et al. [2006]
Gashaka	Nigeria	4.0% (O)	299	12 months	Fowler et al. [2007]
Bulindi	Uganda	10.4% (O), 10.7% (M)	1,436	13 months	This study

TABLE II. Species of Leaf Swallowed by Chimpanzees at Bulindi and their Frequencies in Dung

Plant species	Family	Number of dungs with leaves of species	Percentage of dungs with whole leaves containing species ($N = 149$) ^a	Number of months sp. found in dung ($N = 13$)
<i>Aneilema niasense</i> C.B. Clarke	Commelinaceae	122	81.9%	13 (Jan 07–Jan 08)
<i>Desmodium velutinum</i> (Willd.) DC.	Fabaceae-Faboideae	15	10.1%	6 (Mar, May–Aug, Oct 07)
<i>Lantana camara</i> L. ^b	Verbenaceae	12	8.1%	4 (Sep–Dec 07)
Unidentified grassy leaves	Poaceae (Gramineae)	3	2.0%	3 (Apr, Jun, Nov 07)
<i>Acalypha</i> sp. ^b	Euphorbiaceae	1	0.7%	1 (Nov 07)
? <i>Erythrococca trichogyne</i> ^b	?Euphorbiaceae	1	0.7%	1 (Jun 07)

^aCases do not add up to 100% because five dungs contained leaves of two species.

^bLeaves of genus not previously reported swallowed by wild chimpanzees.

proglottids and two *Oesophagostomum* worms. The majority (10/12) of dungs with adult *Oesophagostomum* were collected in July–December 2007, which included the wettest part of the year. The occurrence of proglottids in dung was more evenly distributed across study months (Fig. 2).

Relationship between Leaf Swallowing and Parasite Expulsion

There was no correlation between proportion of monthly dungs with whole leaves and proportion containing tapeworms ($r_s = 0.181$, $N = 13$, $P = 0.55$) or *Oesophagostomum* worms ($r_s = 0.296$, $P = 0.33$). That is, peaks in leaf swallowing were not associated with peaks in either cestode or adult nematode expulsion. The percentage of dungs with whole leaves that also contained tapeworms (2.7%; $N = 4$) or adult *Oesophagostomum* (2.7%; $N = 4$) was low. Nevertheless, a significant relationship was found between the co-occurrence in dung of whole leaves and adult *Oesophagostomum* (Fisher's exact test, $P = 0.028$). In the case of tapeworms, no relationship was apparent ($P = 0.303$, both tests two-tailed).

Parasites were always recovered loose in dung and were never found between the folds of leaves or attached to the leaf surface. Although consistent records were not made on firmness of dungs, 20% of specimens containing macroscopic parasites were notably diarrheal or semi-diarrheal (nematodes: $N = 5$ cases, tapeworms: $N = 3$, including one dung with both nematodes and proglottids). In contrast, only two dungs with leaves (1.3%) were notably diarrheal and in both cases *Oesophagostomum* worms were also present. These observations suggest that whereas dungs containing whole leaves were not unusual in consistency, parasites in the dung were associated with gastrointestinal upset.

DISCUSSION

Bulindi can be added to the growing list of chimpanzee study sites where leaf swallowing occurs.

Bulindi chimpanzees preferentially ingested whole leaves of *A. niasense*; intact *Aneilema* leaves were present in dung throughout the study. The leaves of two other taxa (*D. velutinum* and *L. camara*) were swallowed occasionally, appearing in dung for limited periods only. All three species are widespread at Bulindi and the leaves of each would have been available to chimpanzees year-round, suggesting the possibility of temporal trends in plant selection. Chimpanzee leaf swallowing involving *L. camara* and *Acalypha* sp. has not previously been reported. Several species swallowed by chimpanzees elsewhere (e.g., *Trema orientalis*, *Ficus asperifolia*, *F. exasperata*, and *F. mucoso*) are not uncommon at Bulindi but the leaves never appeared in dung. Intersite differences in plants used in self-medication could reflect local traditions among chimpanzee populations [Pebsworth et al., 2006]. Alternatively, plants utilized at one site may be ignored at another if other species are available that are more abundant and/or more effective in producing a desired response (e.g., a purging effect).

The overall frequency of whole leaves in dung at Bulindi was considerably higher than in any other population studied to date. Undigested leaves were recovered in dung in each month of the study and leaf swallowing showed no clear seasonality. This conforms to observations elsewhere in Uganda, at Kibale and Budongo, but contrasts with some non-Ugandan sites with prolonged annual dry seasons where peaks in leaf swallowing occurred during wet months [Dupain et al., 2002; Fowler et al., 2007; Huffman et al., 1997; Pruetz & Johnson-Fulton, 2003]. At Mahale, leaf swallowing peaked following the onset of the rainy season when reinfection by *O. stephanostomum* increases [Huffman et al., 1997]. The climate of western Uganda is characterized by a relatively moderate seasonality (bimodal rainfall and lack of a prolonged dry season). Huffman et al. [2009] suggested that climatic differences between habitats affect the life cycle of *Oesophagostomum*, influencing temporal patterns of reinfection and transmission dynamics, and consequently the

self-medicative behavior of chimpanzee hosts. Unlike at Mahale, Budongo chimpanzees did not experience an increase in *Oesophagostomum* infection in wet months [Huffman et al., 2009], which may explain the absence of temporal trends to leaf swallowing there and also further south at Kibale. Data from Bulindi appear to support this hypothesis.

Studies at Mahale and Kibale indicated that chimpanzees swallow leaves in response to infection by nematodes and cestodes, respectively. This is the first report of leaf swallowing in relation to both adult nematode and tapeworm expulsion in one chimpanzee community during the same time period. During a 7-month tapeworm outbreak at Kibale 21.7% of dungs with leaves also contained proglottids [Wrangham, 1995], while at Mahale, *Oesophagostomum* worms occurred in five of six dungs with leaves [Huffman et al., 1996]. In contrast, co-occurrence of leaves and parasites in dung was very low at Bulindi. However, proglottids and adult nematodes can be difficult to detect macroscopically in dung, and potentially some parasites were missed in this study. But this does not explain the low association of leaves and parasites because dungs containing leaves were inspected particularly thoroughly. Since dungs were collected up to an estimated 24 hr following defecation, parasite occurrence was conceivably influenced by the length of time dungs spent on the ground prior to collection. For example, there was some indication that adult nematodes (but not tapeworms) occurred most often in dung estimated to be very fresh (<6 hr). Migration of worms into the soil or incidental predation by birds or other animals cannot be excluded.

Nevertheless, this study demonstrates for the first time a significant relationship between leaf swallowing and expulsion of adult strongyloid nematodes in Ugandan chimpanzees—although the relationship is weaker than at Mahale. Huffman et al. [2009] proposed that the relatively even rainfall distribution at Budongo affects the development and maturation of *Oesophagostomum* in such a way that reduces host pathology associated with encysted larval arrestment in the intestinal mucosa (that characterizes the worm's life cycle in more seasonal environments)—possibly precluding the use of leaf swallowing as a means of purging adult worms from the lumen. Yet forest patches at Bulindi are riverine outliers of the Budongo Forest block (Fig. 1) and climatic conditions are similar, although Bulindi is drier overall (Bulindi: mean annual rainfall = 1461 mm, 2001–2007; Budongo = 1761 mm, 1995–1999, Huffman et al., 2009). Why leaf swallowing should be associated with nematode expulsion at Bulindi but not at nearby Budongo (even though prevalence of *Oesophagostomum* infections were high), requires further investigation.

With regards to tapeworms, there was no relationship between leaf swallowing and the shedding of proglottids at Bulindi, and thus no indication that

this behavior is associated with tapeworm infection. This contrasts with studies at Kibale, where a positive relationship was found [Wrangham, 1995], and at Budongo, where leaf swallowing coincided more frequently than expected in months when proglottids were observed in dung [Huffman et al., 2009]. However, as noted above, dungs were rarely collected immediately following defecation and prevalence rates of macroscopic parasites could have been affected by the time specimens were on the ground. Even so, the low incidence of parasites in dung with leaves implies little about overall infection levels. For example, while parasitological analysis showed that *O. stephanostomum* was the most prevalent nematode infection in Budongo chimpanzees, adult worms were never observed in dung [Huffman et al., 2009]. Unlike tapeworms, for which proglottid expulsion is a part of the organism's life cycle, egestion of adult *Oesophagostomum* is a consequence of the host's immune response, or a behavioral-mediated response to expel them (i.e., self-medication), and is not a requisite stage of the worm's life cycle.

Chimpanzees at Bulindi were experiencing rapid habitat change during this study. Forest fragments were being heavily logged and cleared for agriculture; consequently, contact between people and apes had increased dramatically [McLennan 2010b]. Stress induced by extensive habitat alteration and frequent hostile encounters with people and their dogs [McLennan, 2010a; McLennan & Hill, 2010] could compromise the chimpanzees' immunoresponse system, increasing susceptibility to helminth infections. Alternatively, since these chimpanzees supplement their natural diet with frequent crop raiding [McLennan, 2010b], which presumably confers important nutritional benefits, their susceptibility to infection might be reduced due to improved physical condition, as was suggested for baboons *Papio anubis* at Gashaka, Nigeria [Weyher, 2009] and edge-living *Colobus guereza* at Kibale [Chapman et al., 2006].

Nevertheless, elevated levels of leaf swallowing, occurring year-round, could indicate Bulindi chimpanzees are especially vulnerable to parasite infections, possibly due to environmental changes and/or increased stress levels brought about by their proximity to, and high frequency of contact with, humans. Observations of both macroscopic nematodes and cestodes in dung, but an absence of a strong relationship between leaf swallowing and parasite expulsion, suggest leaf swallowing at Bulindi could be a generalized adaptation to infection by multiple parasites, which may respond differently to the behavior. Since both *Oesophagostomum* and *Bertiella* infection cause abdominal discomfort and gastric disturbances in humans [Brack, 1987; Denegri & Perez-Serrano, 1997], the proximate stimulus for chimpanzee leaf swallowing may be relief from abdominal pain via a purging effect [Huffman et al.,

1996; Wrangham, 1995]. Even so, there was no indication that swallowing leaves induced diarrhea at Bulindi. Increased levels of infection by two parasites, reportedly associated with leaf swallowing at other sites, may be responsible for the higher frequency of leaf swallowing at Bulindi. The stimuli for inducing leaf swallowing could still be directly related to these infections, without always having to result in parasite expulsion.

Oesophagostomum spp. infections are common in wild chimpanzees and prevalence can be high [reaching 100%; Gillespie et al., 2010]. Tapeworm infections appear less common and to date only *Bertiella* sp. has been recorded infecting wild chimpanzees [Ashford et al., 2000; Gillespie et al., 2010; Howells et al., 2011; Huffman et al., 2009; Kawabata & Nishida, 1991]. While chimpanzees at Bulindi were infected with *Bertiella* sp. (probably *B. studeri*), some proglottids were not *Bertiella*, but had a morphology corresponding to *Raillietina* [W. Kabasa, personal communication 2008] or else another cestode of the Davaineidae family [T. Iwaki, personal communication 2011]. While further analysis is required to identify this parasite conclusively (e.g., using molecular methods), it is interesting to speculate on the origin of this putative *Raillietina* infection. *Raillietina* is a common parasite of domestic fowl throughout East and southern Africa [Phiri et al., 2007; Ssenyonga, 1982]. Chimpanzees at Bulindi occasionally preyed on chickens from homesteads bordering forest patches [McLennan, 2010b]. Thus, consumption of infected poultry might be the reason for this possible pseudo-infection [see also Pterzelkova et al., 2006]. Alternatively, chimpanzees could have become infected through ingesting an intermediate insect host.

Our study suggests that longitudinal microscopic parasitological monitoring of both apes and humans at Bulindi is needed for chimpanzee management, and to investigate the potential for disease transmission between apes, people, and their livestock. This is important in view of proposals to establish a wildlife corridor via small forest patches to the west of Bulindi in order to maintain gene flow between chimpanzees in Budongo forest and the Bugoma forest block further south [see McLennan, 2008; Plumptre et al., 2010]. We suggest that the health status of “village” chimpanzees in the intervening region should first be evaluated carefully to minimize risk of introducing novel pathogens into populations in the larger forest blocks.

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