



Self-induced Increase of Gut Motility and the Control of Parasitic Infections in Wild Chimpanzees

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*When physiological adaptation is insufficient, hosts have developed behavioral responses to avoid or limit contact with parasites. One such behavior, leaf-swallowing, occurs widely among the African great apes. This behavior involves the slow and deliberate swallowing without chewing of whole bristly leaves. Folded one at a time between tongue and palate, the leaves pass through the gastro-intestinal (GI) tract visibly unchanged. Independent studies in two populations of chimpanzees (*Pan troglodytes schweinfurthii*) showed significant correlations between the swallowing of whole leaves and the expulsion of the nodule worm *Oesophagostomum stephanostomum* and a species of tapeworm (*Bertiella studeri*). We integrate behavioral, parasitological and physiological observations pertaining to leaf-swallowing to elucidate the behavioral mechanism responsible for the expulsion and control of nodule worm infections by the ape host. Physical irritation produced by bristly leaves swallowed on an empty stomach, increases motility and secretion resulting in diarrhea which rapidly moves leaves through the GI tract. In the proximal hindgut, the site of third-stage larvae (L3) cyst formation and adult worm attachment, motility, secretion and the scouring effect of rough leaves is enhanced by haustral contractions and peristalsis-antiperistalsis. Frequently, at the peak of reinfection, a proportion of nonencysted L3 is also predictably vulnerable. These factors should result in the disruption of the life cycle of *Oesophagostomum* spp. Repeated flushing during peak periods of reinfection is probably responsible for long-run reduction of worm burdens at*

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certain times of the year. Accordingly, leaf-swallowing can be viewed as a deliberate adaptive behavioral strategy with physiological consequences for the host. The expulsion of worms based on the activation of basic physiological responses in the host is a novel hitherto undescribed form of parasitic control.

KEY WORDS: chimpanzee; parasite control; physical mechanism; self-medication; host-parasite relationship.

INTRODUCTION

We integrated new findings and current knowledge of leaf-swallowing behavior in chimpanzees with gut function and life-histories of *Oesophagostomum* spp. to ascertain the mode(s) of action likely responsible for their expulsion by chimpanzee hosts.

Parasitism has played an important role in the evolution of host behavior (Anderson and May, 1982; Clayton and Moore, 1997; Futuyma and Slatkin, 1983). Coevolution between host and parasite has resulted in the development of mechanisms by which the host limits parasitic infection and the parasite increases its chance of infecting the host (Toft *et al.*, 1991; Ewald, 1994). At the primary level, a host's immune response—innate and acquired—normally controls infections; however, some parasites invariably establish themselves by undergoing antigenic variation, thus disguising themselves with the hosts antigens, or by interfering directly with the immune response (Cox, 1993; Wakelin, 1996).

When physiological adaptation is not enough, hosts have developed behavioral responses to avoid or to limit contact with endo- and ectoparasites and other pathogens. These behaviors, which are widespread among the vertebrates, include regularly changing sleeping or feeding sites, differential use of drinking sites, use of antiparasitic leaf material to line nests or dens occupied over long periods, and the application of aromatic substances to repel fur and feather infesting parasites (Baker, 1996; Clark, 1991; Freeland, 1980; Gompper and Holyman, 1993; Hart, 1990; Hausfater and Meade, 1982; Kummer in Nelson, 1960; Seigstadt in Cowen, 1990; Sengputa, 1981). Learned aversion of foods or tastes associated with illness, parasitic infection, and compensatory changes in host dietary preferences induced by parasites are exhibited in the laboratory and field by a wide range of vertebrates (Gustavson, 1977; Kyriazakis *et al.*, 1994; Keymer *et al.*, 1983). The learned aversions are another level at which the host avoids prolonged exposure to pathogens. Dietary modification is another possible means to alter or control internal parasitic load. Rausch (1954, 1961) suggested a causal relationship between a sudden change in diet and reduced tapeworm load in brown bears (*Ursus americanus*). Another example of this type of behavior

involves the ingestion of specific plant parts that have little or no nutritional value for their antiparasitic qualities, which may be either pharmacological (Huffman *et al.*, 1993; 1998; Ohigashi *et al.*, 1994) or physical (Huffman *et al.*, 1996). We will discuss the latter.

Swallowing of whole leaves and subsequent defecation of undigested material was first reported in chimpanzees by Wrangham (1977) and has been investigated subsequently in greater detail by Wrangham and Nishida (1983), Wrangham and Goodall (1989) and Huffman *et al.*, (1996; 1997). Chimpanzees frequently swallowed leaves early in the morning, often as the first or one of the first items ingested (Wrangham and Nishida, 1983; Wrangham and Goodall, 1989). These observations led us to define leaf-swallowing as the slow and deliberate ingestion one by one of whole leaves, which are folded between tongue and palate, and pass through the gastrointestinal tract visibly unchanged. Similar behavior occurs widely in the African great apes; chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and lowland gorillas (*Gorilla gorilla gorilla*) (Huffman, 1997).

Independent studies of the behavior in two populations of eastern long-haired chimpanzees (*Pan troglodytes schweinfurthii*) showed significant correlation between swallowing whole leaves and the expulsion of the strongyle nematode *Oesophagostomum stephanostomum* at Mahale (Tanzania), and a species of tapeworm (*Bertiella studeri*) at Kibale, Uganda (Huffman *et al.*, 1996; Wrangham, 1995). Similar behavior may also have evolved convergently in at least two other vertebrate taxa; the snow goose (*Anser caerulescens*) and the Alaskan brown bear (*Ursus arctos*; Huffman, 1997).

Several ideas have been advanced to explain the early morning habit of leaf-swallowing. All were proposed to explain the effective absorption of a pharmacologically active agent into the body without damage by bright light or stomach pH or to avoid dilution of the agent's effective strength by other foods in the stomach (Newton and Nishida, 1990; Rodriguez and Wrangham, 1993; Wrangham and Goodall, 1989). However, unlike the pharmacological action of pith of *Vernonia amygdalina* that is chewed by chimpanzees apparently for its pharmacological antiparasitic properties (Huffman *et al.*, 1993; 1998; Ohigashi *et al.*, 1994), a primarily pharmacological mode of action for leaf-swallowing, proposed earlier by Rodriguez and Wrangham (1993) has been ruled out for the great apes (Huffman *et al.*, 1996; Messner and Wrangham, 1996; Page *et al.*, 1997). The mode of action appears instead to be based on physical properties of the leaves leading to the expulsion of parasites. However, the significance of swallowing leaves in the early morning and the details of the mechanism of worm expulsion remain unclear (Huffman *et al.*, 1996). Elucidation of this mechanism is crucial to understand this behavior and is expected to enhance understanding of host-parasite interactions.

METHODS AND MATERIALS

Study Site and Subjects

Huffman observed the M group of chimpanzees in the Mahale Mountains National Park, Tanzania with the assistance of Game Officer Mohamedi Seifu Kalunde between 23 November 1993 and 25 February 1994. The study site is on the eastern shore of Lake Tanganyika. The climate is influenced by weather from the lake and the mountainous terrain, which ranges from 772 m at lakeside to 2,500 m above sea level on the mountains. Chimpanzees are supported mainly by the semideciduous gallery forests between 780-1,300 m in elevation. There is a rainy season from approximately mid-October to mid-May (Takasaki *et al.*, 1990). We worked in the early rainy season months because of seasonal peaks in the occurrence of leaf-swallowing behavior (Huffman *et al.*, 1997; Wrangham and Nishida, 1983) and the correlation between the rainy season and a rise in parasitic infections (Huffman *et al.*, 1997), most notably by *Oesophagostomum stephanostomum*.

Behavioral Data and Fecal Collection

We observed subjects by focal-animal and *ad libitum* observations, recording in detail the occurrence of all behaviors. We followed subjects continuously throughout the day until lost or the night nest was made. We noted visible cues to state of health, paying specific attention to deviations in normal activity patterns—frequent resting, suppressed foraging activity, early nesting at night and late exit from the night nest in the morning—involuntary behaviors diagnostic of illness and/or discomfort—coughing, sneezing, flatulence, wheezing and stool type.

We monitored fecal output of the focal subject continuously and as closely as possible. When possible we also monitored the nearest neighbors. We inspected faeces quickly for presence or absence of whole leaves and adult parasitic worms. We collected feces with whole leaves or worms and stored it in plastic bags for further inspection at camp, where we counted the leaves and worms and stored the worms in ethanol.

Concurrently with behavioral notes, we collected fecal samples for parasitological analysis immediately after discharge and placed them individually in 5.0 ml Corning sterile vials. We weighed vials and their contents at camp and prepared and fixed 1-g samples with a 10% neutral formalin solution. We thoroughly mixed contents in the vial before sealed and stored it in a cool dark room. The samples were later microscopically examined at the Kyoto University Primate Research Institute by S. Gotoh. Via the MGL and

McMaster's techniques (expressed as eggs/g feces: EPG), we identified species and measured parasitic loads. We made 3 egg counts for each sample and calculated the EPG for each sample as the mean value derived from those trials.

***Oesophagostomum stephanostomum* in Mahale Chimpanzees**

The nematode parasites of *Oesophagostomum* (Strongyloidea, Oesphagostominae)—nodular worms—are common parasites in the proximal hindgut of pigs, ruminants, primates and rodents. Confusion still exists regarding their taxonomy, but several species of *Oesophagostomum* occur in gorillas (g), chimpanzees (c), and occasionally humans (h) including; *O. bifurcum*, (h, c), *O. aculeatum*, (h), *O. polydentatum* (c, g), and *O. stephanostomum* (c, g, h) (Brack, 1987; Polderman and Blotkamp, 1995; Yamashita, 1963). The species in the gastro-intestinal tract of Mahale chimpanzees has been morphologically identified as *Oesophagostomum stephanostomum* from adult worms by R.C. Anderson, Dept. of Zoology, University of Guelph, Canada and from larvae by J. Blotkamp, Dept. of Parasitology, University of Leiden, The Netherlands (Huffman *et al.*, 1997; Gasser *et al.*, 1999).

A brief summary of the life cycle of *Oesophagostomum*, based on Anderson (1992), is essential to understand the likely impact of leaf-swallowing on the control of infections by the of nodular worms (Fig. 1). Eggs are laid at the 16–32 cell stage. While in the feces, the eggs rapidly develop into L1 rhabditiform larvae, hatching as early as 24 h under optimal conditions. The larvae feed on bacteria and molt to the L2 stage within 24 h of hatching. Within 3–4 days of hatching the L2 molt to become infective L3. L3 retain the protective cuticle of L2 and are capable of surviving long periods of adverse environmental conditions, e.g., hot-dry conditions of the dry season, in a state of dormancy. Infection occurs via ingestion of filariform L3 larvae that are on vegetation eaten by the host. After ingestion, L3 pass to the cecum, where they exsheath within approximately 3 days of ingestion. They then invade the tunica mucosa, stimulating the formation of separate cysts around individual larvae in the gut wall. The larvae develop there to L4 stage, eventually returning to the lumen of the hindgut as immature adults. Adults attach by suction to the mucosal wall, but detach and move freely in search of food and mates.

In adult hosts, which may have developed some degree of immunity to the parasite, tissue reaction may cause larvae to remain in their mucosal cysts. The presence of mature worms in the lumen also inhibits the emergence of

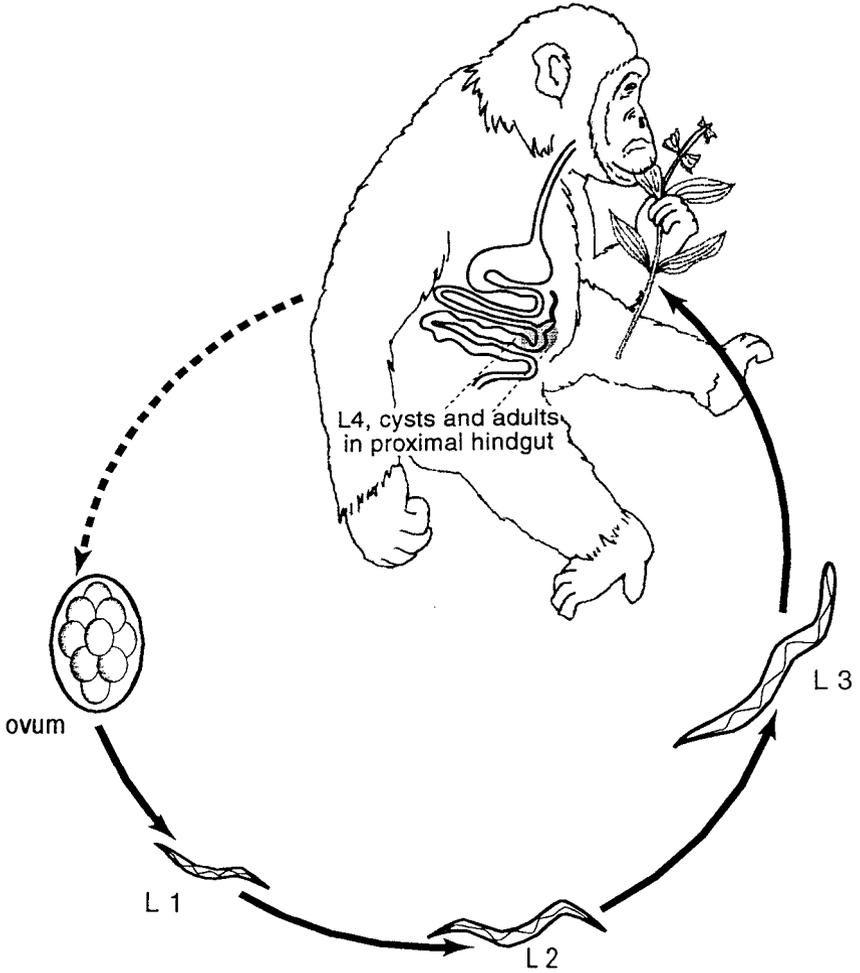


Fig. 1. Life cycle of *Oesophagostomum* spp.

L4 larvae from the nodules (Boch, 1956 cited in Anderson, 1992; Taylor & Michel, 1953). Once in the lumen, the larvae molt and reach the adult stage. Females begin to reproduce and deposit eggs after about one month postinfection.

While infections are carried year-round, reinfection occurs mainly during the rainy season in the Mahale chimpanzees (Huffman *et al.*, 1997). Reinfection, noted by a significant elevation in individual eggs-per-gram (EPG) counts, occurs approximately 1-2 mo after the onset of the rainy season, regardless of which month the rains first begin (Huffman *et al.*, 1997). This lapse

in time corresponds with the 1 mo prepatent period of *Oesophagostomum* spp. (Anderson, 1992). Arrested larval development occurs in *Oesophagostomum* spp. (Armour and Duncan, 1987; Krepel *et al.*, 1994), and at Mahale, shortly after the onset of the rainy season, the external environmental conditions of rising humidity and temperature become optimal for rapid development of the eggs and larvae. The marked rise in individual EPG levels at the beginning of the rainy season is probably due to the increase in transmission by infecting L3 larvae from the environment. However, it is possible that larvae that underwent arrested larval development in the mucosa also play a role. Some nodular worm species are a significant pathogen in domestic livestock, nonhuman primate and occasionally human hosts (Brack, 1987; Karim and Yang, 1992; Lumb *et al.*, 1985; McClure and Guilloud, 1971; Polderman and Blotkamp, 1995; Rousselot and Pellissier, 1952). In humans symptoms of moderate to heavy infections of *Oesophagostomum stephanostomum*, *O. bifurcum* and *O. aculeatum* reportedly range from weight loss, enteritis, diarrhea, anemia and lethargy to anorexia and intense pain simulating appendicitis. Pathology includes hemorrhagic cysts containing larvae, septicemia resultant from bacterial invasion of lesions in the colon, blockage of the colon due to gross thickening of the wall, epigastric or periumbilical masses clearly visible from the outside. Gross lesions in submucosal or subserosal nodules (5–20 mm diameter) are associated with the larvae. These cysts or nodules contain caseous, necrotic centers in a fibrous capsule. Histological findings typically includes intense inflammatory cell reaction accompanied by high levels of neutrophils and eosinophils associated with the nodules (Brach, 1987; Polderman and Blotkamp, 1995; McClure and Guilloud, 1971).

Pathology is believed to be caused only by the encapsulated juvenile worms, not by the adult worms, so a low EPG does not necessarily mean that the host is not affected by some form of pathology. Subsequent reinfection by larvae developing from eggs newly deposited in the feces is no doubt also a contributing factor. Dry season rises in EPG and leaf-swallowing can occur. They are presumably the result of the cessation of arrested larval development within the mucosa (Taylor and Michel, 1953) due to the depression of the host's immune response caused by such factors as secondary illness and food-stress (Huffman *et al.*, 1997), rather than reinfection. Larvae of *Oesophagostomum* spp. can remain dormant within the host for ≤ 1 year (Gordon, 1949). The trends in seasonality of reinfection at Mahale are in close agreement with seasonality in life cycle data from clinical observations of a rural human population in Togo and Ghana infected with *Oesophagostomum bifurcum* (Krepel *et al.*, 1995). Given the severe pathology associated with *Oesophagostomum* species in general, the removal of encysted L3 and L4 stages (Polderman & Blotkamp, 1995; Taylor & Michel, 1953),

or maintenance at low levels or both is a highly-adaptive host strategy for controlling the level of damage caused by the parasites.

RESULTS

Time of Swallowing, Transit Time of Leaves and Stool Type

We recorded 14 cases of leaf-swallowing performed by 12 individuals (Table I). The time of leaf swallowing in the morning or the time leaves first appeared in the feces in the afternoon was closely associated with weather conditions of the previous night and that morning. In general, whole leaves appeared in the feces of chimpanzees later on days when the morning was cloudy and rainy or heavy rains had fallen the previous night than on clear days. Typically chimpanzees stay in their night nests longer on rainy days, likely to avoid the cold and dampness of the underbrush and also because they are likely to have been kept awake by heavy rains in the night. On such days, we observed leaf-swallowing between 0912 and 1035 h ($n = 9$; cases 1–10), and subsequently leaves were in the faeces between 1542 and 1638 h.

A conservative duration calculated from the lower and upper time limits of swallowing and defecation of whole leaves is 6–6.5 h. Subtracting these figures from the lower and upper time range that leaves were in the feces on clear days (ca. 1200–1535 h), an estimated swallowing time on clear mornings is between 0530 and 0900 h. This period fits precisely in the typical waking schedule of Mahale chimpanzees on clear mornings, i.e. between dawn and the time radiant sunlight has reached most areas of the group's home range. This also conforms closely to the data available for Gombe. On average, leaf-swallowing at Gombe occurred around 0715 h and often leaves were the first ingesta of the day in 75% ($n = 40$) of the observations (Wrangham and Goodall, 1989).

Effect on Gastro-Intestinal Function and Transit Time

Leaf-swallowing temporarily induces diarrhea and reduces transit time. Among the 14 cases of leaf-swallowing in Table I, there is a significant relationship between the presence of whole undigested leaves in feces and the occurrence of diarrhea (Fisher's exact test, $p = 0.0472$, $n = 24$). No long-term adverse effects were evident because diarrhea did not persist and the individual's stool type varied throughout the day (Table I).

In 3 cases (3, 9, 13) we closely monitored individuals from the time of leaf-swallowing to the first feces containing leaves (Table I). This

Table 1. Time of leaf swallowing, defaecation without leaves and first time with leaves, stool type and estimate of leaf transit times

Case	Date	Weather ¹	Subject, observation period starts - ends//	Time swallowed (no. leaves)	Time of defaecation ² before leaves appear	Time first leaves appear (leaves, worms)	Estimated TT ³ (h)
1.	10 Jan. 1994	rainy night	AL 09:12//	09:12 - (9+)	no data	no data	
2.	10 Jan. 1994	rainy night	MJ 09:39-13:11	09:39 - (14)	11:19, 12:06	no data	
3.	7 Feb. 1994	rainy, dark	NT 09:55// 13:35-17:16	09:55 - (5+)	not observed	15:56 ⁴ , 15:57* (55,21)	6.02
4.	7 Feb. 1994	rainy, dark	BE 10:00// 10:58-17:31	10:00/ (6+)	12:28, 12:32, 15:56	not observed	
5.	7 Feb. 1994	rainy, dark	IW 10:20// 12:00	10:20/ (9+)	12:00	not observed	
6.	10 Jan. 1994	dark, rainy	LD 10:30//	10:30/ (6+)	no data	no data	
7.	7 Feb. 1994	rainy, dark	JL 10:32//	10:32 - (20)	no data	no data	
8.	7 Feb. 1994	rainy, dark	CY 10:33//	10:33 - (33)	no data	no data	
9.	7 Feb. 1994	rainy, dark	BB 10:35-10:51 // 13:35-17:16	10:35 - (55)	15:54	16:38*	6.3
10.	8 Feb. 1994	dark, cloudy	BE 11:41-16:10	not observed	not observed	15:42* (4, 0)	4.02 → 8.5 ⁵
11.	19 Feb. 1994	clear	NT 11:40-15:30	not observed	not observed	11:58* (1, 2) 15:27	
12.	6 Feb. 1994	clear	DE 09:23-14:51	not observed	12:40	12:45* (not counted, many)	3.4 → 5.5 ⁵
13.	25 Nov. 1993	clear	MU 08:11-15:10	08:00-08:10	8:37, 9:45, 9:47, 12:14, 12:23	13:44* (not counted, many)	5.6
14.	27 Dec. 1993	clear	TL 09:31-17:50	not observed	10:50	15:07, 15:36* (18 : 18)	5.6

¹Weather conditions of previous night and early morning leaf swallowing was observed.

²Stool type: italicized times are diarrhea otherwise stools were firm. *worms found in dung.

³Estimation of TT calculated from the observed time of leaf-swallowing (or the onset of focal observations) to first time defaecation of leaves was observed. There estimates (cas nos. 3, 9, 13) are considered the best approximations of TT in this study based on direct evidence.

⁴Observations started approximately 10 m after subject climbed down from night nest.

⁵A djusted estimate of TT derived by subtracting average leaf swallowing time of 7:15 on clear mornings from first time leaves were observed in dung.

measurement is the digesta transit time (Warner, 1981). The estimated transit time (TT) for these 3 cases ranged from 5.5 to 6.3 h, which agrees closely with the conservative calculated range based on observed morning swallowing times and independently observed afternoon defecation times on rainy days. Two of the estimates for TT on clear days were notably shorter (3.5–4.8 h). This may be due to the fact that observations did not begin until late morning (Table I). If the figures are corrected by calculating TT based on an average clear day, swallowing time of 0715 h (mean of the estimated range of clear day swallowing time), the resultant TT in both cases (5.5 h; 8.5 h) closely fits the general trend. The mean of estimates of TT in Table I is TT 6.2 h (SD 1.1, n = 6) for swallowed whole leaves. When leaves are swallowed whole first thing in the morning on an empty stomach, there is ≥ 17.4 h reduction in TT versus the digesta transit of 23.6 h (SD 2.4, n = 8) for a fruit meal, fed to captive chimpanzees (Idani, 1986). The estimated (6.23 ± 1.15 h, n = 6) and best approximate TT (5.97 ± 3.5 h, n = 3) means are in close agreement.

It cannot be overstressed that these are estimates of the upper and lower limits of TT for whole leaves swallowed by chimpanzees in our study. TT modified by leaf-swallowing is expected to vary depending upon the total number of leaves swallowed and certainly upon whether or not the individual had eaten other foods before leaf-swallowing. Due to small samples size we are unable to evaluate the possible effect of the number of leaves swallowed on the variability of TT.

Impact of Leaf-Swallowing on Parasitic Load

The presence of adult *Oesophagostomum stephanostomum* in the feces of Mahale chimpanzees is an extremely rare event in any situation (3.7%, 9/245, Huffman *et al.*, 1997). However, when in feces of individuals on days when they swallowed leaves, they were most likely in the feces with whole leaves (Fisher's Exact Test, $p = 0.0001$, n = 24; Table I). Live adult *Oesophagostomum stephanostomum* were in the liquid fecal material or trapped within the folded leaves. On average, there were 10.3 worms (SD 10.8, range 2–21) with 19.8 leaves (SD 25.6, range 1–55) per stool, at a rate of 0.54 worms per leaf expelled via leaf-swallowing (n = 4; Table I). There are discrepancies, however, in each case between the number of leaves we saw subjects swallow and the number of leaves subsequently recovered from their feces (Table I). Accordingly, the figures are conservatively low estimates of the possible immediate impact of leaf-swallowing on worm burden.

We know of no data on total worm burdens of *Oesophagostomum stephanostomum* in wild chimpanzees. For *Oesophagostomum bifurcum* in

humans, an average burden of 96 worms (SD 89.06, range 12–300, $n = 12$) can occur in rural people of Togo and Ghana (calculated from Table I. of Kreple and Polderman, 1992). Extrapolating from our data, theoretically a chimpanzee would need to pass at least 176 leaves or engage in leaf-swallowing on average 10 times over the rainy season to rid itself of a comparable worm burden. The actual number of leaves swallowed by an individual in a single case ranged from 5 to 55. This scenario suggests that repeated swallowing of leaves by chimpanzees over consecutive days or weeks could have a significant impact on their overall worm burden. A more decisive approximation of total impact would require controlled clinical testing of chimpanzees infected with predetermined worm burdens, but, due to ethical considerations such a study is not feasible.

DISCUSSION

Hypothesized Mechanism of Leaf-Swallowing for the Expulsion of *Oesophagostomum stephanostomum*

Three factors are important to understand the effects of leaf-swallowing on the gastro-intestinal tract of the chimpanzees and ultimately on the parasites in the proximal hindgut, namely, the timing of leaf-swallowing, increased rate of digesta transit, and the diarrhea associated with the appearance of leaves in the feces. Much is known about the function of the gastro-intestinal compartments of *Homo sapiens*, and it is reasonable to assume that the chimpanzee gut functions similarly. This assumption is based on the similarities in gastro-intestinal morphology, and the close phylogenetic relationship of the two species. The gastro-intestinal tract can be divided into three distinct units. Regulation of the activity of each of them is independent of the others, nevertheless the physiological state of another gut compartment influences the others through neurochemical mechanisms (Guyton, 1976; Weisbrodt, 1987).

The patterns of motility in each gastro-intestinal units and the timing of leaf-swallowing behavior are crucial to understand the effect of the leaves on the gut. Leaf-swallowing commonly occurs before the first meal of the day (Wrangham and Goodall, 1989; Huffman *et al.*, 1996). The stomach and small intestine of the chimpanzees would have emptied overnight, so that the interprandial pattern of slow waves of contraction—myo-electrical activity—would have been established in them (Weisbrodt, 1987; Malgelada and Azpiroz, 1989). Swallowing the leaves would immediately stimulate the full stomach pattern of increased secretion and motility. The contractions of the external muscle layer would thus bring the rough surfaces of the leaves

into direct contact with the gastric mucosa causing physical irritation. This effect would be enhanced by emptiness of the stomach. The presence of the mucosal irritant would have two effects, which are part of a protective mechanism for the removal of potentially damaging substances (Guyton, 1976):

1. increased secretion of highly acidic gastric juice;
2. increased motility of the hindstomach allowing the leaves and secretions to pass quickly through the pyloric sphincter into the small intestine.

The rate of movement of the leaves through the small intestine would also be rapid and would be accompanied by an increase in secretion (Guyton, 1976; Malagelada and Azpiroz, 1989). Clearly digesta transit time is increased by leaf-swallowing (Table I). The TT of seeds from fruit meals in captive chimpanzees was approximately 23.6 h (Idani, 1986). The mean transit time of a particle marker (chromium mordanted to cell wall constituents) in chimpanzees fed a commercial diet ranged from 37.7 to 48.0 h, depending on the fiber content of the diet (Milton and Demment, 1988). Comparison of these results with times in wild chimpanzees after leaf-swallowing shows that there is a marked reduction in the estimated transit time for a single meal (Table I).

Whole leaves, with their abrasive surfaces and the corrosive mixture of secretions that accompany them, would be emptied into the proximal hindgut, thereby stimulating increased secretion and motility there. The pattern of movement of the cecum and proximal colon is different from that of the small intestine. It consists of alternating bouts of peristalsis and antiperistalsis, as well as localized mixing movements within individual haustra (Elliott and Barclay-Smith, 1904; Christensen, 1989; Caton, 1997). The movements of the leaves back and forth, as well as within the haustra, would help to dislodge the worms. Also, even subtle changes in the environment of the lumen can have significant impact on establishment and persistence of *Oesophagostomum* in the host (Petkevicius *et al.*, 1999). Any resultant change in the contents of the lumen, caused by secretions of acid and enzymes from the stomach, plus enzymes from the small intestine, are likely to affect adult worms as well as any pre-encysted L3 larvae in the lumen. The contents of the hindgut would be evacuated rapidly before there is a chance for the reabsorption of water, resulting in the diarrhea that is often associated with leaf-swallowing. Prolonged bouts of leaf-swallowing would produce a continual source of irritation.

The control-of-nematode-infection hypothesis (Huffman *et al.*, 1996; 1997) predicts that since nodular worm infections are typically self-limiting (Beaver *et al.*, 1984), the total infection may be controllable if a chimpanzee

responds to the symptoms during the most likely period of reinfection. Based on the observed physiological response of the gut to whole rough leaves and details of the life cycle of *Oesophagostomum*, we conclude that the most probable mechanism explaining the control of nematode infection (Huffman *et al.*, 1996) results in at least three areas of antiparasitic action (Fig. 2); 1) adult worm detachment and expulsion, 2) flushing out a proportion of the incoming infective L3 larvae before they are able to exsheath and penetrate the mucosa, and 3) decreasing pathology of cysts (and reducing discomfort) by inducing the emergence of juvenile larvae into the lumen. This process, repeated continually during peak periods of reinfection should result in a lowering of overall infection and control the number of debilitating cysts.

A Convergent Evolutionary Strategy for the Expulsion of Intestinal Parasites?

Leaf-swallowing has also been associated with the presence of tapeworm proglottids in feces of chimpanzees, geese and bear and with roundworms in dogs. Wrangham (1995) demonstrated that passing whole leaves through the gut increases the probability of tapeworm fragments being shed by chimpanzees at Kibale.

Observations of undigested plant leaf material (*Carex* sp. Cyperaceae) and large masses of tapeworms in the feces of Alaskan brown bears in the late fall by Barrie Gilbert (Department of Fisheries and Wildlife, Utah State University) led him to suggest that grass swallowing may be responsible (Huffman, 1997). In hibernating grizzly bears, Parasitic levels, in particular tapeworms and ascarids, are quite low or absent (Rausch, 1954; 1961). The fact that grass-swallowing in bears occurs before hibernation suggests a causal relationship.

John Holmes (Parasitology, Department of Biological Sciences, University of Alberta) has observed a similar phenomena in Canadian snow geese. In the summer prior to their migration south, juvenile birds in particular, carry significant tapeworm burdens. Also at this time of year, Holmes and his colleagues observed large boluses of undigested grass and tapeworms in goose faeces. When they measured the parasite loads of these same flocks after migrating south, the middle to lower guts were found to be completely void of tapeworm infection; no scolices were found (J. Holmes, personal communication in Huffman, 1997).

AE Makundi (Veterinarian, Faculty of Veterinary Medicine, Sokoine University, Morogoro, Tanzania) has observed the expulsion of roundworms (*Ascaris toxicara*) by dogs swallowing grass (personal communication to M.A.H).

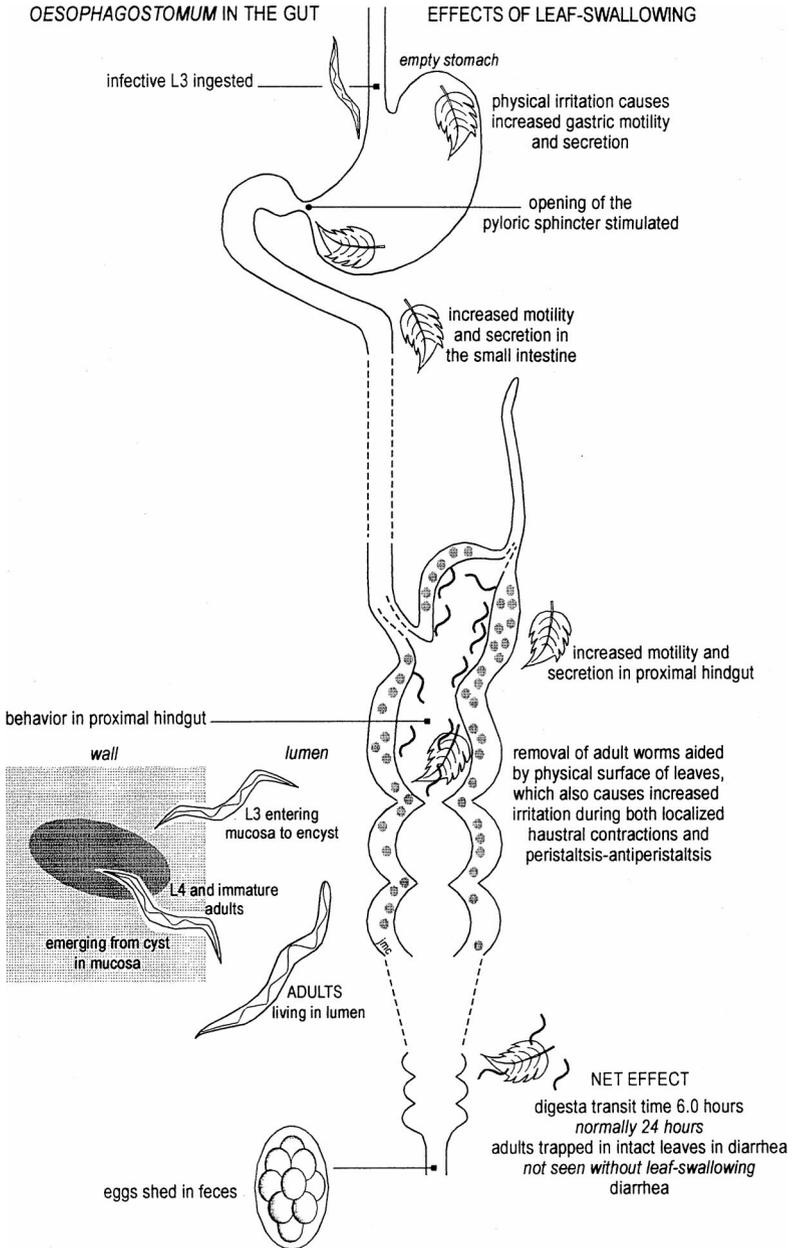


Fig. 2. The proposed mechanism of leaf-swallowing and its effect on infections with *Oesophagostomum* at different stages of the life cycle.

Given the wide phylogenetic diversity of these three species it is possible that such an adaptation occurs among a much wider range of vertebrates infected with these and other gastro-intestinal parasites. We predict that increased transit time induced by a leaf-swallowing like behavior will play a significant role in any host with similar gut function infected with *Oesophagostomum* spp.

CONCLUSIONS

1. Control of infections by repeatedly flushing out worms during peak periods of infection is thought to lead to the long-run reduction of worm burdens.
2. Repeated flushing of the GI tract is predicted to disturb the life cycle of *Oesophagostomum* spp. at three key stages of the life cycle; reducing new L3 infections taking hold in the mucosa, removing mature adult worms from the lumen and, encouraging encysted L4 and immature adults to exit into the lumen, whereupon they are removed from the gastro-intestinal tract of the host.
3. Leaf-swallowing is a deliberate action that is an adaptive behavioral strategy with physiological consequences for the host apparently lacking an efficient immunological defense against a parasite's virulence to the host.
4. Leaf-swallowing is a strategy which may have convergently evolved in several vertebrate taxa.
5. This non-pharmacological expulsion of worms based on the activation of basic physiological responses in the host is a novel hitherto undescribed mechanism of parasite control.

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