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Regurgitation and remastication in the foregut-fermenting proboscis monkey (*Nasalis larvatus*)

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Although foregut fermentation is often equated with rumination in the literature, functional ruminants (ruminants, camelids) differ fundamentally from non-ruminant foregut fermenters (e.g. macropods, hippos, peccaries). They combine foregut fermentation with a sorting mechanism that allows them to re-masticate large particles and clear their foregut quickly of digested particles; thus they do not only achieve high degrees of particle size reduction but also comparatively high food intakes. Regurgitation and remastication of stomach contents has been described sporadically in several nonruminant, nonprimate herbivores. However, this so-called ‘mericism’ apparently does not occur as consistently as in ruminants. Here we report, for the first time, regurgitation and remastication in 23 free-ranging individuals of a primate species, the foregut-fermenting proboscis monkey (*Nasalis larvatus*). In one male that was observed continuously during 169 days, the behaviour was observed on 11 different days, occurred mostly in the morning, and was associated with significantly higher proportions of daily feeding time than on days were it was not observed. This observation is consistent with the concept that intensified mastication allows higher food intake without compromising digestive efficiency, and represents an expansion of the known physiological primate repertoire that converges with a strategy usually associated with ruminants only.

Key words: rumination, mericism, foregut fermentation, herbivory, food intake

1. INTRODUCTION

Primate species appear to cover the full variety of trophic niches – from nearly exclusive folivory to frugivory, insectivory, gummivory, omnivory [1] and the nearly exclusive carnivory observed in some human cultures [2]. Primates are also represented in nearly all

major morphophysiological herbivore digestion types, where symbiotic microbes are hosted in a ‘fermentation chamber’ in the gastrointestinal tract to digest plant fibre – caecum fermenters (maybe even coupled with coprophagy [3] as observed in nonprimate caecum fermenters), colon fermenters, and nonruminant foregut fermenters [4-7]. The only major strategy of herbivores not described in primates so far is the regurgitation and remastication of digesta. Such behaviour has been observed sporadically in macropods [8-10] and the koala (*Phascolarctos cinereus*)[11-13], and is a physiological fixture of ruminant foregut fermentation.

Although nonruminant foregut fermentation, including that found in primates, has been termed ‘ruminant-like’ and explicitly or implicitly equated with ruminant foregut fermentation [14,15], there is a major difference between the two modes of foregut fermentation. The foregut of functional ruminants is equipped with a density-dependent sorting mechanism [16] that not only ensures that large particles are regurgitated for rumination, but also that small digested particles leave the foregut at a faster rate, thus clearing the forestomach and facilitating high food intakes compared to nonruminant foregut fermenters [17,18]. Nonruminant foregut fermenters are constrained in their food intake level for the following reason [18]. High food intake is generally associated with shorter digesta retention times in the gut, which may compromise the efficiency of microbial digestion of fibre. This is not a problem in hindgut fermenters, where easily digestible nutrients are first digested in the small intestine by the host’s enzymes (a process that is not under a relevant time constraint), and fibre is subsequently digested in the hindgut by the microbes’ enzymes; the latter part of digestion may be either more thorough (in a low intake-long retention strategy) or less thorough (in a high intake-short retention strategy). In foregut fermenters, the microbes will digest both, fibre and those nutrients that the host could potentially digest with its own enzymes, before the digesta reaches the size of auto-enzymatic digestion, the small intestine.

Because the digestion of non-fibrous substrates by microbes is much faster than that of fibre, yet energetically less efficient for the host than auto-enzymatic digestion, a high intake-short retention strategy would leave a foregut fermenter with the worst of both ways: easily fermentable substrates are digested at reduced efficiency, but fibre is digested incompletely due to insufficient retention. Clauss et al. [18]. recently termed this predicament the ‘foregut fermentation trap’. It also appears to apply to primates, where hindgut fermenters cover the whole range of intake-retention strategies, whereas foregut fermenters are constrained to a low intake-long retention strategy [19]. Reducing food particle size could be one strategy to alleviate this constraint, because smaller particles can be digested by microbes at a faster rate [20].

Proboscis monkey are the largest foregut-fermenting primates and ingest a diet consisting of various proportions of leaves and fruit [21]. They are endemic to Borneo and inhabit mangroves, swamps and riverine forests. Here, we report regurgitation and remastication behaviour in this species that has, so far, not been documented.

2. METHODS

Between January 2000 and March 2001 we recorded proboscis monkey behaviours along a tributary of Kinabatangan River, Malaysia (5°30’N/118°30’E) using videocamera event sampling [22]. We identified 8 one-male groups and 1 all-male group totalling 47 adults, 21 subadults, 83 juveniles and 43 infants, and collected their behavioural data from a boat on the river in the early morning (total behavioural video recordings: 92h) and late afternoon (102h) while monkeys were at riverside trees. From May 2005- 2006 we observed a well-habituated identifiable one-male group (1 adult male, 6 adult females, 9 immatures) for a total of 3507h using focal animal sampling [21,23]. Whether the same individuals as 2000-2001 were observed was unknown. During this second period, continuous observations facilitated calculation of time budgets of adult monkeys, including the proportion of the day spent feeding, and time spent feeding on individual food items.

3. RESULTS

In 2000-2001, regurgitation/remastication (R/R) was observed at least once in 23 different individuals (5 adult males, 10 adult females, 6 subadults, 2 juveniles). R/R occurred soon after the abdomen contracted (Fig. 1a), and the tongue was extruded outside from a pursed mouth (Fig. 1a-c). Regurgitated material was kept in the mouth, extending the cheeks (Fig. 1bc), was masticated and swallowed again. Usually, this behaviour was consecutively repeated several times. In the group that was observed continuously in 2005-2006, R/R was not observed in any female, but on 11 occasions on 11 different days in the adult male. R/R occurred in the morning, before beginning a new feeding bout, in nine and in the afternoon in two of these observations. R/R lasted 1.0-8.7 minutes (mean [SD] 5.1 ± 4.9 min), representing $2.3 \pm 1.8\%$ of the adult male's total feeding time. The mean percentages of time spent feeding was significantly higher (U-test: $U=583$, $p=0.01$) on days where RR was observed ($n=11$, mean [SD] $27.5 \pm 6.6\%$, range 16.2-36.5) compared to days where it was not observed ($n=158$, mean [SD] $20.1 \pm 8.3\%$, range 9.8-45.1). The difference was not related to variation in the time spent feeding on a particular food category. The differences in time spent feeding on main diet items did not differ between days with and without R/R (young leaf: $71.4 \pm 26.2\%$ vs. $71.4 \pm 30.6\%$, $U=872$, $p=0.93$; fruit: $21.7 \pm 22.9\%$ vs. $15.8 \pm 24.6\%$, $U=1006.5$, $p=0.33$; flowers $6.6 \pm 11.2\%$ vs. $10.9 \pm 17.1\%$, $U=712.5$, $p=0.31$, respectively), indicating that the change was rather due to a generally higher intake than to the high intake of a particular diet item.

4. DISCUSSION

To our knowledge, these are the first records of a naturally occurring R/R behaviour in primates. Although regurgitation/reingestion has been described in gorillas (*Gorilla gorilla*)[24], it is not linked to an adaptive physiological process but is considered pathological, and does not occur in free-ranging animals. In humans, 'merycism' or 'rumination disorder' is considered an abnormal condition that affects adults, but in particular

infants or intellectually handicapped individuals, and is sometimes related to eating disorders
 [25]. R/R or merycism, as a physiological phenomenon, has so far only been investigated
 systematically in koalas [11], where it represented on average 3.9 % of total feeding time. R/R
 was reported to occur particularly under two conditions in koalas, where it either compensated
 for a lack of masticatory efficiency due to progressed tooth wear in old age [13], or in
 lactating females, where it potentially compensated for the digestibility-reducing effect of
 increased food intake [12]. Our observations on R/R in proboscis monkey, where the
 behaviour occurred both in males and females, adults and juveniles, excludes these two
 possibilities as explanations; instead, we can only speculate that the behaviour served to allow
 for an increased food intake under yet-to-be-specified conditions. Because the behaviour has
 so far only been reported here in groups of one particular habitat, we cannot exclude a
 behavioural tradition [26] among proboscis monkeys in our case (that would nevertheless
 serve its physiological purpose). Our observations indicate that regurgitation and
 remastication is well within the scope of possible adaptations within the primates'
 physiological repertoire, but it may not be sufficiently common to be of physiological
 relevance for a species in general. Foregut fermenters may benefit particularly from such a
 behavioural option, as it may help them to relieve the constraints of the 'foregut fermentation
 trap'. Preliminary data on particle size reduction in captive animals [27] indicates a trend that
 foregut fermenting primates have adaptations for a more distinct particle size reduction,
 achieving relatively finer faecal particles than other primates (mean [SD] relative faecal
 particle size $0.47 \pm 0.07 \text{ mm kg}^{-0.22}$ in four foregut fermenting species vs. $1.27 \pm 0.76 \text{ mm kg}^{-0.22}$
 in 17 other species; U-test $p=0.049$). More detailed studies on the occurrence of R/R among
 primate species, and its physiological and ecological connotations, remain to be performed.

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For video sequences of described behaviour see Electronic supplement.

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Figure 1 Stills from video recordings (see Electronic supplement for full videos) in two female (a, b) and a male (c) proboscis monkeys (*Nasalis larvatus*). Note in female a) the contraction of the abdomen that leads to a lifting of the thorax prior to regurgitation. All individuals display a protruding tongue prior to re-mastication, and in the second female b) and the male c), the protruding cheeks are clearly visible.

Short title: Remastication in proboscis monkeys

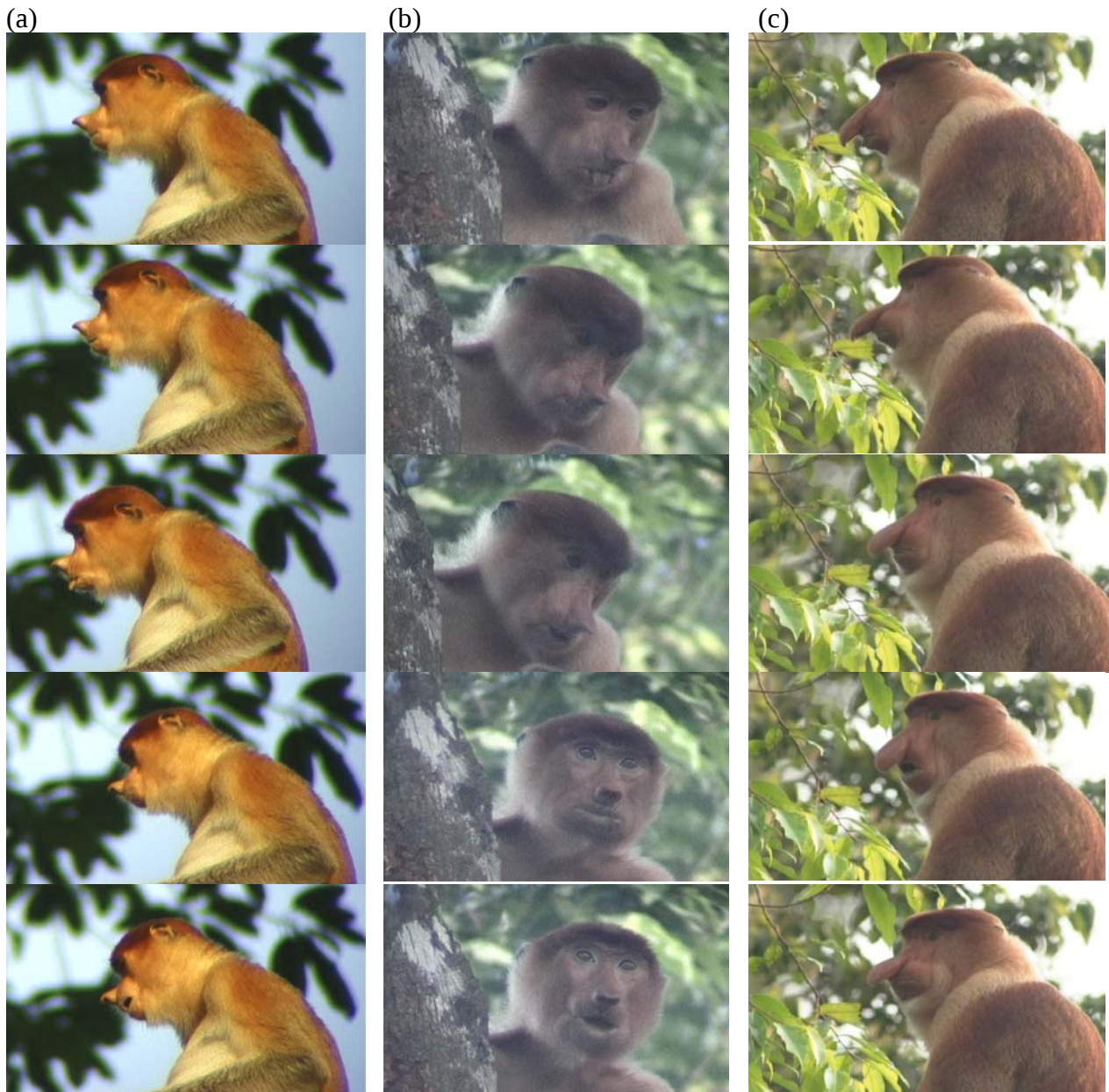


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