

1 Research Article for Biology Letters

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

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

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

37

38 **1. INTRODUCTION**

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

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

50 Although nonruminant foregut fermentation, including that found in primates, has been
51 termed ‘ruminant-like’ and explicitly or implicitly equated with ruminant foregut fermentation
52 [14,15], there is a major difference between the two modes of foregut fermentation. The
53 foregut of functional ruminants is equipped with a density-dependent sorting mechanism [16]
54 that not only ensures that large particles are regurgitated for rumination, but also that small
55 digested particles leave the foregut at a faster rate, thus clearing the forestomach and
56 facilitating high food intakes compared to nonruminant foregut fermenters [17,18].
57 Nonruminant foregut fermenters are constrained in their food intake level for the following
58 reason [18]. High food intake is generally associated with shorter digesta retention times in
59 the gut, which may compromise the efficiency of microbial digestion of fibre. This is not a
60 problem in hindgut fermenters, where easily digestible nutrients are first digested in the small
61 intestine by the host’s enzymes (a process that is not under a relevant time constraint), and
62 fibre is subsequently digested in the hindgut by the microbes’ enzymes; the latter part of
63 digestion may be either more thorough (in a low intake-long retention strategy) or less
64 thorough (in a high intake-short retention strategy). In foregut fermenters, the microbes will
65 digest both, fibre and those nutrients that the host could potentially digest with its own
66 enzymes, before the digesta reaches the size of auto-enzymatic digestion, the small intestine.

67 Because the digestion of non-fibrous substrates by microbes is much faster than that of fibre,
68 yet energetically less efficient for the host than auto-enzymatic digestion, a high intake-short
69 retention strategy would leave a foregut fermenter with the worst of both ways: easily
70 fermentable substrates are digested at reduced efficiency, but fibre is digested incompletely
71 due to insufficient retention. Clauss et al. [18]. recently termed this predicament the ‘foregut
72 fermentation trap’. It also appears to apply to primates, where hindgut fermenters cover the
73 whole range of intake-retention strategies, whereas foregut fermenters are constrained to a
74 low intake-long retention strategy [19]. Reducing food particle size could be one strategy to
75 alleviate this constraint, because smaller particles can be digested by microbes at a faster rate
76 [20].

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

81

82 **2. METHODS**

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

92

93 **3. RESULTS**

94 In 2000-2001, regurgitation/remastication (R/R) was observed at least once in 23 different
95 individuals (5 adult males, 10 adult females, 6 subadults, 2 juveniles). R/R occurred soon after
96 the abdomen contracted (Fig. 1a), and the tongue was extruded outside from a pursed mouth
97 (Fig. 1a-c). Regurgitated material was kept in the mouth, extending the cheeks (Fig. 1bc), was
98 masticated and swallowed again. Usually, this behaviour was consecutively repeated several
99 times. In the group that was observed continuously in 2005-2006, R/R was not observed in
100 any female, but on 11 occasions on 11 different days in the adult male. R/R occurred in the
101 morning, before beginning a new feeding bout, in nine and in the afternoon in two of these
102 observations. R/R lasted 1.0-8.7 minutes (mean [SD] 5.1 \pm 4.9min), representing 2.3 \pm 1.8% of
103 the adult male's total feeding time. The mean percentages of time spent feeding was
104 significantly higher (U-test: U=583, p=0.01) on days where RR was observed (n=11, mean
105 [SD] 27.5 \pm 6.6%, range 16.2-36.5) compared to days where it was not observed (n=158, mean
106 [SD] 20.1 \pm 8.3%, range 9.8-45.1). The difference was not related to variation in the time
107 spent feeding on a particular food category. The differences in time spent feeding on main
108 diet items did not differ between days with and without R/R (young leaf: 71.4 \pm 26.2% vs.
109 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
110 6.6 \pm 11.2% vs. 10.9 \pm 17.1%, U=712.5, p=0.31, respectively), indicating that the change was
111 rather due to a generally higher intake than to the high intake of a particular diet item.

112

113 4. DISCUSSION

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

119 infants or intellectually handicapped individuals, and is sometimes related to eating disorders
120 [25]. R/R or merycism, as a physiological phenomenon, has so far only been investigated
121 systematically in koalas [11], where it represented on average 3.9 % of total feeding time. R/R
122 was reported to occur particularly under two conditions in koalas, where it either compensated
123 for a lack of masticatory efficiency due to progressed tooth wear in old age [13], or in
124 lactating females, where it potentially compensated for the digestibility-reducing effect of
125 increased food intake [12]. Our observations on R/R in proboscis monkey, where the
126 behaviour occurred both in males and females, adults and juveniles, excludes these two
127 possibilities as explanations; instead, we can only speculate that the behaviour served to allow
128 for an increased food intake under yet-to-be-specified conditions. Because the behaviour has
129 so far only been reported here in groups of one particular habitat, we cannot exclude a
130 behavioural tradition [26] among proboscis monkeys in our case (that would nevertheless
131 serve its physiological purpose). Our observations indicate that regurgitation and
132 remastication is well within the scope of possible adaptations within the primates'
133 physiological repertoire, but it may not be sufficiently common to be of physiological
134 relevance for a species in general. Foregut fermenters may benefit particularly from such a
135 behavioural option, as it may help them to relieve the constraints of the 'foregut fermentation
136 trap'. Preliminary data on particle size reduction in captive animals [27] indicates a trend that
137 foregut fermenting primates have adaptations for a more distinct particle size reduction,
138 achieving relatively finer faecal particles than other primates (mean [SD] relative faecal
139 particle size $0.47 \pm 0.07 \text{mm kg}^{-0.22}$ in four foregut fermenting species vs. $1.27 \pm 0.76 \text{mm kg}^{-0.22}$
140 in 17 other species; U-test $p=0.049$). More detailed studies on the occurrence of R/R among
141 primate species, and its physiological and ecological connotations, remain to be performed.

142
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 146 conducted in compliance with animal care regulations and applicable Malaysian laws.

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148 For video sequences of described behaviour see Electronic supplement.

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 219

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

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Short title: Remastication in proboscis monkeys

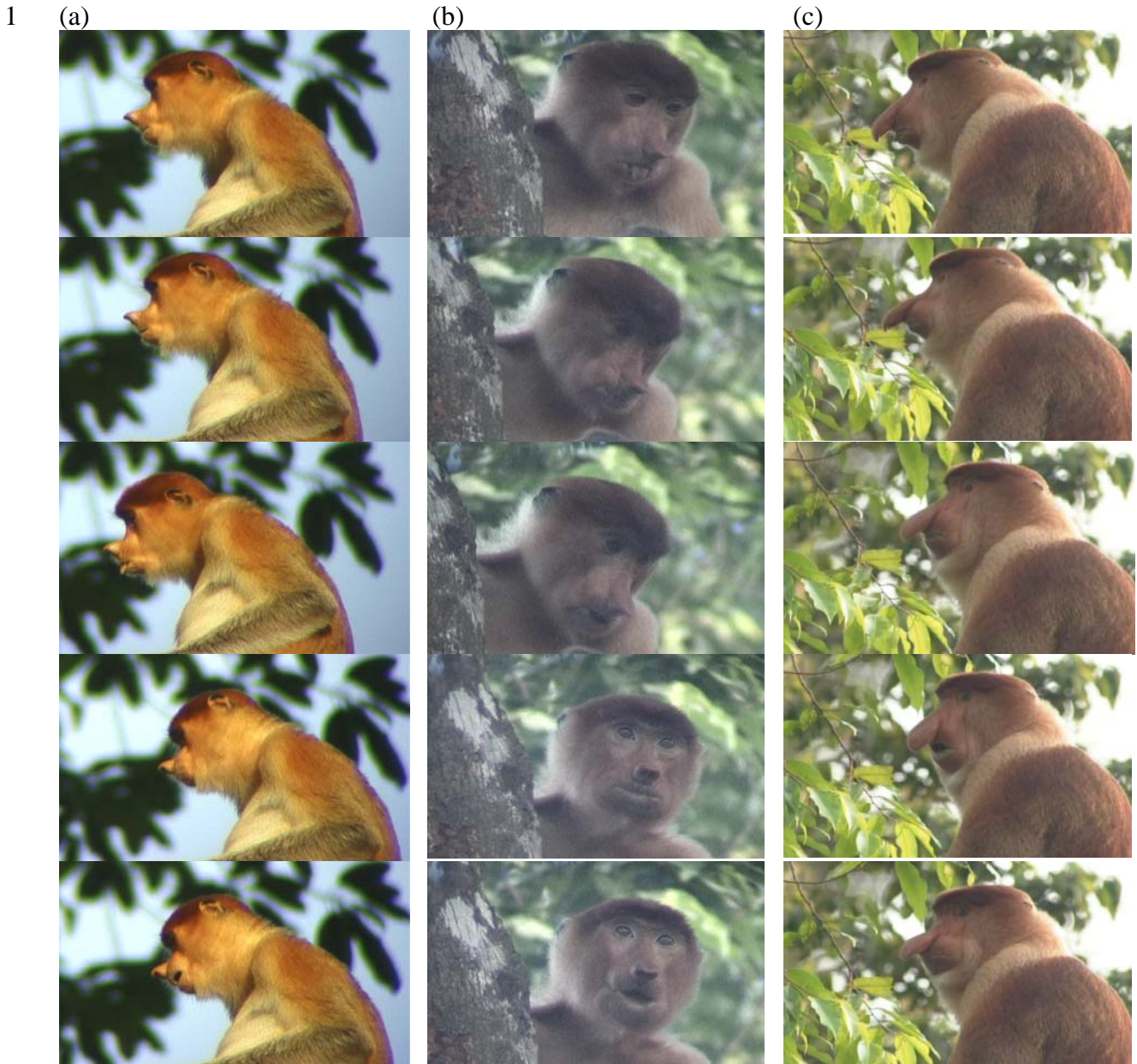


Figure 1 Stills from video recordings (see Electronic supplement for full videos) in two female (a, b) and a male (c) proboscis monkeys (*Nasalis larvatus*). Note in female a) the contraction of the abdomen that leads to a lifting of the thorax prior to regurgitation. All individuals display a protruding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