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Evidence for the occurrence of rumination-like behaviour, or merycism, in the koala (*Phascolarctos cinereus*, Goldfuss)

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Abstract

This paper provides the first account of merycism in koalas (*Phascolarctos cinereus*), and in doing so, potentially sheds new light on the occurrence and significance of this behaviour in other herbivorous marsupials. Koalas fitted with acoustically sensitive transmitters, to monitor mastication and ingestive behaviour, were also found to make bouts of rhythmic 'mastication-like' noises that were not associated with ingestive feeding events. On average, these bouts consisted of 9.16 'mastications', at an average rate of 1.21 'mastications' per second, and occurred 53.3 times throughout a 24-h period. Furthermore, bouts were usually preceded by, and always followed by, a series of 'creaky', guttural noises that were interpreted as regurgitation and re-swallowing, respectively. Merycism may allow koalas to periodically re-masticate gastric digesta, while in a resting position, and thus potentially save energy and increase the extent of food preparation. Consequently, merycism may contribute to the koala's ability to consume a high fibre, poor quality diet.

Key words: Koala, merycism, rumination, feeding ecology, *Phascolarctos cinereus*

INTRODUCTION

Rumination is the regurgitation, re-mastication and re-swallowing of gastric digesta, however, the term is usually only used to refer to such processes in ruminants and camelids. The mechanics and biological significance of rumination have been well studied, and are discussed by Gordon (1968), Van Soest (1994) and Stevens & Hume (1995). Plant material consumed by ruminants is initially swallowed after having been only partly masticated, thus allowing this material to be ingested rapidly. Some of this material is later regurgitated into the mouth as a bolus of softer, partly digested ingesta, where it is extensively re-masticated. Stevens & Hume (1995) described the regurgitation phase as an involuntary act that begins with inspiration against a closed glottis (resulting in a negative pressure in the oesophagus), followed by aspiration of digesta from the rumen into the thoracic oesophagus by the relaxation of the gastroesophageal sphincter. Finally, the digesta moves into the mouth by an anti-peristaltic wave of oesophageal contraction. Rumination increases fibre digestibility as well as stimulating the secretion of buffered saliva to assist in the titration of the volatile fatty acids produced by the forestomach bacteria. Furthermore, Gordon (1968) estimated that grazing cattle spend up to one-third of the day ruminating and that sheep, by ruminating in a recumbent position, conserve up to 10% of their daily energy intake.

Early studies into regurgitation by macropods (reviewed in Hume, 1982; Langer, 1988) and dasyurids (Fleay, 1961; Archer, 1974), describe this activity as a violent heaving of the chest and abdomen that results in the stomach contents being forced up into the mouth, before either being immediately re-swallowed (usually without any additional mastication), or else completely ejected. Whilst anatomists initially considered regurgitation in macropodines to be analogous to rumination, Barker, Brown & Calaby (1963) were insistent that macropods do not ruminate, and preferred the term 'merycism'. Merycism (from the Latin *merycismus*, meaning 'rumination'), is used to refer to the sequence of regurgitating, re-masticating and re-swallowing observed in mammals in general (including man), and is not suggestive of the form of digestive processes it precedes, as has become the case with the term 'rumination'.

Dellow (1979) observed that the frequency of merycism in macropods could be increased by adding crushed grain to a diet of chopped hay. It was proposed that the addition of grain increased the rate of fermentation, thereby lowering the pH of digesta in the forestomach. Dellow (1979) therefore proposed that merycism may aid digestion in macropodines by stimulating saliva secretion (which would have a buffering effect on the forestomach, as in ruminants), rather than by increasing food mastication.

Moir, Sommers & Waring (1956), described a second

form of jaw movement, which occurs more frequently than merycism, and which they claimed did not involve the regurgitation of a food bolus. These rhythmic jaw movements were observed in kangaroos that were resting in the lying posture, and often occurred several hours after the animal had ceased feeding. Dellow (1979) suggested that these prolonged periods of rhythmic jaw movements, may (like merycism) have a role in stimulating salivary secretion.

The debate over whether any marsupials demonstrate merycism has been confounded by inconsistencies in what is considered to be merycism behaviour. Whilst the rhythmical jaw movements described by Moir *et al.* (1956), in the apparent absence of regurgitation, are not considered to be merycism, the violent regurgitations in the absence of re-mastication, are considered merycism. This reflects the realization that re-mastication necessarily follows regurgitation, and the potential misconception that regurgitation events are always clearly observable actions. However, these irregular, violent heaving actions, along with the absence of any additional mastication, are indicative of emesis (vomiting), in which material is pushed (rather than aspired) into the oesophagus by an abdominal press (Stevens & Hume, 1995). In addition, Owen (1835) noted that these acts occurred more frequently following the administration of a physic, further suggesting an expulsion rather than rumination-like process. Therefore, based on its definition, merycism should only be used to refer to a sequence of regurgitation, re-mastication, and subsequent re-swallowing of digesta.

In an ongoing investigation (pers. obs.) into the effects of tooth wear on mastication and feeding ecology, free-ranging koalas *Phascolarctos cinereus* were found to engage extensively in non-feeding 'mastication' events. The koala is an arboreal marsupial that feeds almost exclusively on the mature foliage of *Eucalyptus* trees (Pratt, 1937). These leaves are low in protein, are physically difficult to process, are highly defended chemically, and at times toxic (Cork & Sanson, 1990). Allometric scaling from a range of mammalian herbivores (Demment & Van Soest, 1985), indicates that koalas are highly stressed energetically. Their ability to use such a poor quality diet is believed to result from their low metabolic requirements (Nagy & Martin, 1985), and their highly developed caecum and proximal colon (MacKenzie, 1918).

The purpose of this paper is to provide some evidence for the occurrence of pseudo-rumination, or merycism, in koalas, and to comment on its potential importance in the mechanical preparation of plant material for digestion and fermentation.

METHODS

Six male koalas of varying ages, were captured from a wild population on Raymond Island (off Victoria, Australia), and fitted with newly developed, acoustically sensitive radio transmitters (Sirtrack Ltd). Transmitters were powered by 'C'-sized lithium batteries and attached to wildlife collars such that the microphones were positioned under the chin of the animal, in close proximity to the throat. Each individual was released within 10 min of capture into the tree from which it was captured, and periodically monitored for an additional 3 days to assess its condition and well-being. During this time, attempts were made to calibrate all the sounds received from the transmitters against observed koala activities. Thereafter, each individual was randomly allocated to 2 of the next 12 days, during which all the sounds that it made over a continuous 24-h period (commencing at 16:00), were recorded.

Sounds made by each koala over 2 separate, yet continuous 24-h periods were recorded onto 5-h video tapes using a Panasonic Long-Play VCR via a Uniden Bearcat hand-held scanner and elevated Discone, omnidirectional antennae. Video tapes were later analysed aurally to identify and quantify each of the sounds for each 24-h recording period. Masticatory bouts could be clearly identified and were defined as 3 or more mastications that were spaced no more than 5 s apart, and that were not interrupted by any other audibly recognizable activities. Average mastication rates were calculated by dividing the number of consecutive mastications by the elapsed time (in s) for each bout, and dividing this by the number of bouts. Similarly, the rates of other audibly distinguishable activities were determined. A paired *t*-test carried out using SYSTAT (Wilkinson, 1990), was used to statistically compare the rates of ingestive mastications to merycism 'mastications'.

Periods of wakefulness were defined as a period of time in which the animal made regular (< 2 min apart) 'awake' noises. These 'awake' noises included: climbing; walking; feeding; scratching; vocalizing; or movement of the head or limbs (each of which were audibly distinct and discernible).

RESULTS

All individuals were found to make bouts of rhythmic, mastication-like noises that were not associated with feeding events. These bouts occurred at irregular intervals whenever the animal was awake. Whilst these noises sounded very similar to the regular ingestive masticatory noises detected by the transmitters (indicating molar occlusion), the rate of these other 'mastications' was significantly slower than regular mastications ($t_{(n=6)} = 59.504$, $P > 0.001$), see Table 1. Furthermore, bouts of these 'mastication-like' noises occurred irregularly, yet frequently (Table 1), throughout the 24-h recording periods, and were not associated with any other food manipulation or biting sounds.

Averaged across each of the six individuals, there were 9.16 (± 1.32) of these other mastications per bout, compared to 30.23 (± 4.99) mastications per mouthful of leaf material whilst feeding. When expressed as a

Table 1. Comparison of the masticatory characteristics of merycism and ingestive feeding related mastications in koalas *Phascolarctos cinereus*. Mastication rate (mastications s^{-1}), averaged across the six individuals per 24-h. A bout of feeding represents the number of mastications per mouthful. All numerical parameters expressed as the mean (± SD) of the six individuals for two separate, yet continuous 24-h recording periods

Mastication type	Mastication rate	Mastications per bout	Bouts per 24-h	Associated sounds
Ingestive feeding	2.42 (± 0.13)	30.23 (± 4.99)	834.3 (± 94.2)	Food manipulation leaf incising, branch rustling, climbing
Merycism	1.21 (± 0.10)	9.16 (± 1.32)	53.3 (± 19.7)	No ingestive feeding associated sounds, preceded and followed by guttural 'creak'

percentage of the total number of mastications recorded per 24-h, these other mastications constituted up to 9% of an individual koala's total daily occlusal events. These bouts were usually proceeded by a series of guttural throat noises (creaky-door like), and were always immediately followed by a single similar noise.

DISCUSSION

Whilst Moir *et al.* (1956) had no way of determining whether the 'jaw movements' they observed involved tooth–tooth contact, the sounds obtained in this study clearly indicate deliberate molar occlusion, and thus, 'masticatory' events. However, they are clearly different from ingestive mastications, having a significantly slower 'mastication' rate, and on average consisting of 70% fewer 'mastications' per bout. Therefore, it is likely that these 'mastication-like' events are also functionally different to the mastications associated with the initial ingestion of food material. Furthermore, these 'mastication-like' events were not found to be associated with any other regular feeding noises such as food manipulation, biting of leaves, rustling of branches and ingestive masticatory noises. In fact, these other 'mastication' noises were frequently made by individuals that were resting in either dead trees or trees of a non-food species, and therefore had no access to fresh leaf material. Dental inspection of koalas captured during this study also often (6/45, 13.3%) revealed the presence of partly masticated plant material in their mouths, even when the koalas were captured from dead trees during the middle of the day. Consequently, it was concluded that they were most probably re-masticating previously ingested food material.

It is acknowledged that the above findings do not constitute unequivocal evidence for the occurrence of merycism in koalas as the presence of food material in the mouth during this other form of 'mastication' has yet to be confirmed. It is possible that these other jaw movements represent 'thegosis'. Thegosis (from the Greek, *thego* to whet or sharpen) is the proposed process of attritional tooth sharpening caused by tooth–tooth contact that is independent of masticatory function (Every, 1974). However, many workers (reviewed in Murray & Sanson, 1998) have challenged both the evidence for such a tooth sharpening mechanism in mammals, as well its functional significance. Furthermore, extensive lateral striations on the cristids and cristae wear facets of koala molars (Young & Robson, 1987) suggest that there is little pure tooth–tooth contact. To confirm whether or not koalas regurgitate and re-masticate food material, an experiment needs to be performed in which a captive animal is fed labelled food before being placed in an X-ray chamber, and monitored for an extensive time period. Such an experiment is likely to be very stressful for the animal, and therefore considered ethically and scientifically unsound.

The frequency with which these non-feeding, 'mastication-like' bouts (hereafter referred to as re-mastication) occurred (on average 53.3 times/24-h) strongly suggests that koalas regularly re-masticate their food material. Each bout of re-mastication was usually preceded by a series of 'creaky', guttural noises. Although it was not possible to determine the exact nature of these noises, the proximity of the microphone to the mouth, and its direct contact with the throat, did suggest origins in the back of the throat. Likewise, these re-mastication bouts were always followed by a single, similar throat noise, which may represent a subsequent swallowing event. These noises could represent respectively, the regurgitation and re-swallowing of food material. Based on these findings, it would seem reasonable to propose that koalas practise merycism. Furthermore, its frequency of occurrence suggests that it may be important in the mechanical preparation of food material for digestion and fermentation.

Dellow (1979) argued that the rhythmical jaw movements of resting kangaroos described by Moir *et al.* (1956), may increase the flow of saliva, and thus, by buffering the forestomach, be an advantage during periods of extensive fermentation. Koalas however are hindgut fermenters. Consequently, additional salivary secretions resulting from jaw movements, are unlikely to assist in pH buffering within the fermentation chambers of the hindgut. In fact, koalas have a large cardiogastric gland on the lesser curvature of the stomach (MacKenzie, 1918), which is believed to enhance acid production in the stomach (Milton, Hingson & George, 1968). This would suggest that a low stomach pH is not a limitation to digestion. Moreover, given the potential costs of tooth wear (Lanyon & Sanson, 1986*b*), it would

also seem unlikely that koalas would occlude their teeth to the extent recorded in this study, if it did not directly assist in the preparation of food material.

Neither regurgitation nor re-mastication have previously been reported in koalas. This is despite the large amount of attention they have received, particularly with respect to their feeding ecology. The frequent guttural noises that accompanied bouts of the proposed re-mastication in koalas, were relatively quiet, seemingly gentle, and were often not associated with the obvious movement of other external body parts. This might indicate that pre-ingested food material is regurgitated in small quantities, rather than as a large bolus. Hence, several of these regurgitations might occur, thereby resulting in a gradual accumulation of food material in the mouth, before a bout of re-mastication is stimulated. The small number of 'mastications' per bout (compared to ingestive mastications) also suggests that the quantity of food material processed was substantially smaller than for initial ingestion.

The morphology and function of koala cheek teeth have been described extensively by Lanyon & Sanson (1986*a*). They illustrated the ratchet-like manner in which leaves are moved across the cheek teeth at a steady rate of one molar row width per occlusial stroke. In koalas with relatively unworn teeth, this results in comminuted leaf particles having evenly serrated edges that match those of the teeth, and dimensions that correspond to the lateral distances between the cutting edges. Hence, leaf material is thought to make only one pass of the teeth, before being swallowed. Once a feeding bout is complete, the koala usually moves to a more stable part of the tree, where it spends a considerable amount of time resting (Nagy & Martin, 1985). It is while in this position, that most of the re-masticatory events described in this study were recorded. Hence, like ruminating, this strategy of supplementing rapid ingestion by re-masticating in a resting posture potentially saves the animal considerable amounts of energy.

The biological significance of merycism has received little attention. This is probably partly because of the perception that non-ruminants masticate their food adequately on initial ingestion (Barker *et al.*, 1963), that regurgitation events are considered relatively rare, and to the inconsistencies in what is considered merycism behaviour. As proposed in this investigation, merycism might actually be a frequent activity, but one that might also be very subtle and not easily detected. Consequently, merycism might be more commonly practised than is currently acknowledged. Furthermore, when it occurs to the degree demonstrated here in koalas, merycism is potentially important.

Perhaps more significantly, this is the first record of rumination-like behaviour in a hindgut fermenter. The strategies and merits of foregut and hindgut fermentation are discussed by Alexander (1993). Unlike foregut fermenters, which derive most of their energy from the bacterial fermentation of cell walls, hindgut fermenters derive most of their energy from the cell contents, and mastication is believed to occur only on the ingestive phase. Koalas are considered to be highly specialized hindgut fermenters. Although it is estimated that koalas only derive *c.* 9% of their energy from the fermentation of cell wall (Cork & Hume, 1983), the extent of caecum and proximal colon development (MacKenzie, 1918) suggests that this is important. Furthermore, to maximize the rate of fermentation, fine material is also selectively retained in the caecum, whilst the larger, less fermentable particles are shunted though the gut more rapidly. These specializations emphasize the importance of cell wall fermentation in the nutritional ecology of koalas, and thus also emphasize the importance of appropriate food preparation. The ability to re-masticate food material may enable koalas to process their food material more finely, thereby exposing more cell contents and increasing the rate and extent of fermentation. In addition, this can be completed in a resting position, thereby saving energy. Hence, in conjunction with low metabolic requirements and extensive caecum and colon development, merycism may contribute to the ability of koalas to use their poor quality diet.

In conclusion, acoustically sensitive transmitters revealed that koalas engage in frequent, relatively regular 'mastication-like' bouts that differ substantially from regular masticatory events in 'mastication' rate, the number of 'mastications' per bout, and in the absence of other feeding associated noises. It is therefore proposed that koalas practice merycism, the action of regurgitating, re-masticating and re-swallowing previously ingested food material. Analogous to rumination in ruminants and camelids, merycism may allow koalas to periodically re-masticate gastric digesta while in a resting position, and thus potentially save energy and increase the extent of food preparation.

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