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EFFECT OF TOOTH WEAR ON THE RUMINATION-LIKE BEHAVIOR, OR MERYCISM, OF FREE-RANGING KOALAS (*PHASCOLARCTOS CINEREUS*)

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Rumination-like behavior, or merycism, of 5 adult male koalas (*Phascolarctos cinereus*) with various degrees of tooth wear was investigated using acoustically sensitive radio telemetry. Increased tooth wear was associated with a significant increase in mean rate of merycism mastication, mean number of merycism mastications per bout per 24 h, and mean number of mastications per 24 h. The ratio of mean number of ingestive mastications to mean number of merycism mastications per 24 h remained approximately 17:1 with increasing tooth wear. These results suggest that in contrast to true rumination, alterations in merycism behavior may be important in compensating for reduced molar effectiveness.

Key words: feeding compensations, koalas, merycism, *Phascolarctos cinereus*, rumination, tooth wear

Recently, the occurrence of rumination-like behavior, or merycism, in free-ranging koalas (*Phascolarctos cinereus*) was described by Logan (2001), who suggested that koalas regurgitate, remasticate, and reswallow small amounts of preingested leaf material. In ruminants, rumination reduces ingested food material to the critical particle size necessary to exit the rumen (Poppi et al. 1981). It also allows food material to be ingested quickly and then remasticated later in a recumbent position, thereby saving energy (Gordon 1968) and potentially reducing the risks of predation.

In mammalian herbivores, nutrient and energy uptake is dependent on the extent to which food material is processed (McLeod and Minson 1969; Pearce and Moir 1964), which in turn depends on the effectiveness of the masticatory apparatus (Perez-Barberia and Gordon 1998a) and thus the morphological integrity of the molars and premolars. Increased tooth wear reduces effectiveness of mastication and has a demonstrable effect on the ingestive behavior of herbivorous mammals where it has been measured (e.g., Logan and Sanson 2002; Perez-Barberia and Gordon 1998b). However, effects on different animals vary greatly and appear to reflect major differences in digestive strategies.

In red deer (*Cervus elaphus*, a ruminating foregut-fermenter), a decrease in masticatory effectiveness (increased tooth wear) resulted in reduced voluntary food intake (Perez-Barberia and Gordon 1998b). In the ruminant digestive system, the passage of comminuted (reduced through mastication) food particles is delayed by a reticular–omasal orifice that restricts the size of the particles that can pass through to the stomach. The rate at which particles are reduced by mastication and microbial action therefore determines the gut passage rate. Consequently, reduced masticatory effectiveness results in an increase in retention time and thus a decrease in passage rate and intake. In contrast, koalas (*P. cinereus*) are hindgut fermenters that compensate for tooth wear by increasing the amount of leaf material consumed and the number of mas-

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tications per unit of food (Logan and Sanson 2002). Along with the selective retention of fine particles and an increase in gut passage rate, increasing food intake and number of mastications per unit of food potentially maintains a constant fill of fine particles in the cecum and proximal colon, thereby partly offsetting the effects of reduced molar effectiveness.

Koalas feed almost exclusively on the high-fiber, low-nutrient foliage of eucalyptus trees. The ability of koalas (<15 kg) to use such a poor quality diet has been attributed partly to their highly developed cecum and proximal colon and selective retention of fine particles therein (Cork and Warner 1983). Such specializations emphasize the important role that cellulose fermentation plays to the nutritional ecology of koalas. Consequently, merycism may enable ingested food material to be processed more completely, thereby increasing the proportion of finer particles presented to the small intestine and thus increasing the rate and extent of fermentation and digestion of ingested foliage. Furthermore, like rumination, merycism can be performed at a later time (while recumbent) when the material has been partly softened, thereby potentially saving substantial amounts of energy. Therefore, it might be expected that koalas with increased tooth wear also increase merycism behavior so as to offset the effects of reduced masticatory effectiveness. Hence, the aim of this study was to investigate the effects of tooth wear on the degree and rate of merycism mastications in free-ranging koalas.

Materials and Methods

Procedure.—This study was conducted in conjunction with investigations (Logan and Sanson 2002) into the consequences of tooth wear on the feeding behavior of free-ranging koalas. Five adult male koalas (*P. cinereus*) with various degrees of tooth wear were captured from a wild population on Raymond Island, approximately 300 km E of Melbourne, Australia (38°55′S, 147°45′E). Each koala was weighed (±100 g) and fitted with a transmitter collar containing an acoustically sensitive audio transmitter (Greager et al. 1979; Lentle et al. 1998; Logan and Sanson 2002) before being released within 15 min of capture into the tree from which it had been captured. Weights of adult individuals, listed from low to high tooth wear, were 10.0, 11.3, 10.4, 10.4, and 10.4 kg, and all individuals were in good body condition.

To evaluate tooth wear, the jaws of an individual were kept open during dental inspection using a V-shaped, rubber-coated bar placed in the diastema. Tooth wear was evaluated according to the description in Martin (1981) and was further confirmed using the descriptions in Lanyon and Sanson (1986) and Gordon (1991). Tooth wear represented a scale potentially ranging from 0.0 (unworn) to 7.0 (completely worn or absent). When features of premolar wear were between the classes described by Martin (1981), fractional scores depicting the degree of deviation from each class were used (e.g., features of wear class 4.5 were between those of classes 4 and 5). Although tooth wear is often used with various degrees of success to estimate age classes of animals (Gipson et al. 2000), in the present study, tooth wear was investigated for its potential to reduce energy and nutrient intake rather than to act as a surrogate for age determination. The exact age of the koalas used in this study was not known.

After a period of at least 72 h after release, in which koalas used in this study were able to recover and transmitted sounds could be calibrated against observed activities, sounds made by each individual were recorded for 2 separate, yet continuous, 24-h periods (commencing at 1600 h) onto BASF PHG300 video cassette recorder (VCR) tapes using a long-play Panasonic NV-HD620 VCR (Panasonic, Japan). A more complete description of the study site, capture procedure, and field equipment is given in Logan and Sanson (2002), and the acoustic differences between ingestive and merycism mastications are highlighted in Logan (2001).

Video cassette recorder tapes were later replayed in real time and in synchrony with event-recording software written by the author. Each audibly recognizable event was digitally flagged along with the exact time and date at which it occurred. Ingestive and merycism mastications, which represent the mastications associated with initial food intake and reprocessing of regurgi-

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tated ingesta, respectively, were identified and distinguished on the basis of descriptions found in Logan (2001). The resulting digital data were manipulated to calculate the total number of ingestive mastications per individual per day (24 h) and the following masticatory parameters of merycism per individual per day (24 h): mastication rate (mastications per second), mastications per bout, and total number of mastications. Logan (2001) defined mastication bouts as 3 or more mastications spaced no more than 5 s apart. For each individual for each 24 h, the number of merycism mastications also was expressed as a ratio against the number of ingestive mastications. Each of the performance parameters of merycism was expressed as a mean per individual for the 2 separate, yet continuous, recording sessions.

Data analysis.—Linear regression analyses (Sokal and Rohlf 1981) were performed to determine the effect of increased tooth wear on the daily mean rate of merycism mastications (mastications per second), mastications per bout, number of mastications, and number of merycism mastications relative to total number of mastications. Regressions were generated with SYSTAT (Wilkinson 1990), with criterion for statistical significance set at $P < 0.05$ for each analysis. Assumptions of normality and homescedasticity were met in all cases.

Results

Increased tooth wear was found to be associated with a significant increase in the mean number of merycism mastications per 24 h ($r^2 = 0.887$, $d.f. = 1$, $P = 0.017$; Fig. 1a), mean number of merycism mastications per bout per 24 h ($r^2 = 0.986$, $d.f. = 1$, $P = 0.002$; Fig. 1b), and mean merycism mastication rate per 24 h ($r^2 = 0.909$, $d.f. = 1$, $P = 0.012$; Fig. 1c). The individual with the highest degree of tooth wear performed 75% more merycism mastications per 24 h, masticated at an 18% higher rate, and masticated 37.5% more per bout than the individual with the lowest degree of tooth wear. The ratio of ingestive mastications to merycism mastications was relatively constant with increasing tooth wear and averaged approximately 17:1 (Fig. 1d). Hence, merycism mastication constituted 6% of total number of mastications (ingestive and merycism) in all koalas.

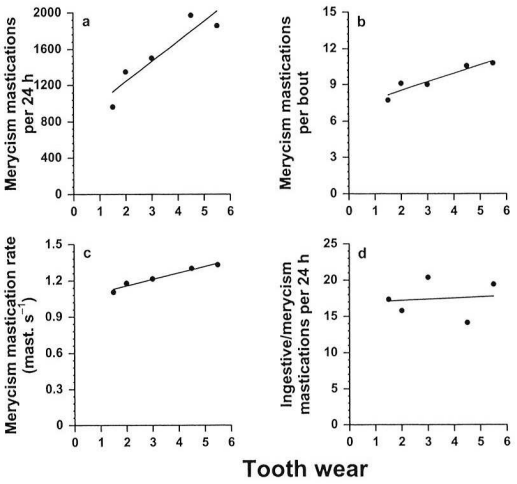

FIG. 1.—Relation of merycism to tooth wear in koalas (*Phascolarctos cinereus*) as shown by a) number of merycism mastications per 24 h, b) number of merycism mastications per bout per 24 h, c) merycism mastication rate per 24 h, and d) number of ingestive mastications per 24 h divided by number of merycism mastications per 24 h, against tooth wear. Curves represent regression on tooth wear. Each point represents mean of 2 separate, yet continuous, 24-h recording sessions for a single individual; $n = 5$.

Discussion

Although the results are based on a small number of individuals, they suggest a strong association between merycism behavior and the degree of tooth wear. The consequences of increased tooth wear on merycism in koalas are similar to those that affect ingestive feeding behavior. That is, it is likely that the increase in merycism mastications was caused by the increase in initial food consumption (resulting in an increase in material to be potentially reprocessed) and a need to masticate more per unit of food material comminuted as a result of lower molar effectiveness. Although it is tempting to speculate that the increased number of merycism mastications per bout represents such an increase in mastications per unit of food regurgitated, unlike the

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food material that is initially ingested, it was not possible to determine the quantity of food material regurgitated for bouts of merycism. However, it is reasonable to suggest that if teeth are less effective at preparing material on initial ingestion, they are also less effective at remasticating the material during bouts of merycism.

Although koalas do not possess a gastric sieve through which the passage of ingested particles out of the rumen is controlled, as found in large ruminants (Perez-Barberia and Gordon 1998b), they selectively retain fine particles in the cecum and proximal colon for further fermentation and pass larger, less fermentable particles out more rapidly (Cork and Warner 1983). However, rather than being a threshold selector, as is possibly the case in large ruminants, the koala may select by gradation whereby the finer the particle, the greater the probability of retention. Therefore, whereas rumination emphasizes a balance between particle retention and eventual passage through the ruminal sieve (Cork 1994), selective retention and merycism in the koala appear to emphasize the reduction of some material as fine as possible so as to maximize cecal fill of fine particles.

Allometric scaling from a range of herbivorous mammals suggests that a high ratio of metabolic rate to gut capacity should restrict small herbivores (<15 kg) to relatively low-fiber diets (Demment and Van Soest 1985). However, recent studies have highlighted the ability of some small herbivores to digest fiber as efficiently as larger herbivores (Conklin-Brittain and Dierenfeld 1996; Gordon and Illius 1996; Justice and Smith 1992), thereby appearing to bend the "allometric rules" (Foley and Cork 1992).

Koalas are small (<15 kg) hindgut fermenters that consume a high-fiber diet and are therefore highly specialized. In conjunction with low metabolic requirements, fermentation rates are maximized by a greatly enlarged hindgut in which fine particles are selectively retained. Logan (2001) suggested that by further reducing the size of food particles, merycism may contribute to the ability of koalas to use such a poor quality diet. If so, an increasing degree of merycism would also help offset the effects of tooth wear by assisting in the maintenance of fine-particle production.

Blue duikers (*Cephalophus monticola*) compensate for a high-fiber diet of willow leaves by increasing intake and spending more time ruminating and harvesting (Wenninger and Shipley 2000). Hence, small ruminants may compensate for the prohibitively slow fermentation rates associated with diets high in fiber by increasing gut passage rate (perhaps through a relatively large reticular–omasal sieve), by chewing food material more finely, or both. These mechanisms may be also associated with greater exploitation of more readily digestible cell contents, as is the strategy used by some small nonruminant foregut fermenters (Cork 1994). Because small ruminants appear to respond to increased fiber in a way similar to other small nonruminants, they also may compensate for reduced masticatory effectiveness by increasing, rather than decreasing, harvesting, rumination, and passage rates.

Ingestive mastication rates are higher than remastication rates in koalas (Logan 2001) and red deer (Perez-Barberia and Gordon 1998b). The rate at which an animal masticates appears to be related to the interaction between properties of the material being comminuted and ability of the masticatory apparatus to reduce the food material and create a bolus. In the present study, increased tooth wear was associated with an 18% increase in the rate of merycism mastications from the individual with the lowest degree of tooth wear to the individual with the highest degree of tooth wear. This is similar to the 15% increase in ingestive chew rate for the same individuals reported by Logan and Sanson (2002). They suggested that altering the rate at which the leaf material is sheared may alter the fracture properties of that material,

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thereby enabling effectively different shearing blades to produce similar shearing results when occluded at different rates. If we assume that, as in initial ingestion, the properties and quantities of material being comminuted in merycism are the same for each individual, differences in rate also may be attributed to the differential abilities of teeth of differing morphologies to process food.

Although merycism mastications were found to make up only 6% of total number of mastications, this does not necessarily mean that they are unimportant. The hindgut of koalas has been described as one of the most highly developed, yet cell-wall fermentation contributes only 9% of total daily energy for koalas (Cork and Hume 1983). Hence, the degree of hindgut specialization emphasizes the importance of this 9%. Likewise, although constituting only 6% of total daily mastications, merycism may make an important contribution to energy uptake in koalas. Furthermore, the slower rate of occlusion during merycism (compared with ingestion) may signify a subtle difference in the nature of occlusion. If so, an alteration in occlusal stroke rate combined with altered structural properties of the food material resulting from a period of gastral occupation may alter the shearing properties of remasticated food material. Alternatively, a slight alteration in occlusal path or force may result in remasticated food material being procured in a different manner. Either way, a single merycism mastication may be as effective at reducing food material as multiple ingestive mastications and may thus contribute more to food reduction than the measurable 6%.

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