

The effect of tooth wear on the feeding behaviour of free-ranging koalas (*Phascolarctos cinereus*, Goldfuss)

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Abstract

The free-ranging feeding behaviours of five adult koalas *Phascolarctos cinereus* with varying degrees of tooth wear were investigated using acoustically sensitive radio telemetry. An increase in tooth wear was found to be associated with a significant increase in the average amount of time spent feeding, average number of leaves consumed and the average number of daily chews. This suggests that koalas compensate for tooth wear by increasing food intake. Furthermore, there was a significant increase in the average number of chews per leaf and average chew rate, suggesting a greater investment in processing each leaf.

Key words: tooth wear, feeding ecology, compensations, koala, *Phascolarctos cinereus*

INTRODUCTION

Herbivores derive most of their energy from plant material either through the endogenous breakdown of cell contents (Keys, Van Soest & Young, 1969) and/or microbial fermentation of cell walls (Prins & Kreulen, 1990). The rates of both *in vitro* and *in vivo* fermentation are known to be affected by the size of the food particles presented to the microflora (Pearce & Moir, 1964; McLeod & Minson, 1969). Latham *et al.* (1978) suggested that it was the increased area of damaged cell wall that promoted greater microbial attachment which was responsible for accelerating cell wall fermentation. Hence, both the rate and extent of fermentation are a function of food preparation. The dentition of a hind-gut fermenter is thus important both in rupturing cell walls to release cell contents, and in increasing the surface area of cell walls to maximize microbial fermentative digestion.

The dentition of the koala has been well described (Stirton, 1957; Archer, 1978; Strahan, 1978; Lanyon & Sanson, 1986a), and reflects, in its morphological complexity, the physical difficulties of processing mature eucalypt foliage (Lanyon & Sanson, 1986a). An efficient shearing action is achieved through the possession of high, tightly interlocking cusps with opposing long, curved blades (Lanyon & Sanson, 1986a), the integrity of which are important in maintaining this masticatory effectiveness (Lanyon & Sanson, 1986b). However, the

abrasive properties of the leaf material, along with the actions of processing such material, cause the teeth to wear down. This wearing alters the tooth morphology (Martin, 1981; Lanyon & Sanson, 1986a), thereby potentially jeopardizing masticatory effectiveness, and ultimately reducing the availability of nutrients and the rate of fermentation in the small intestine.

Tooth wear has been shown to affect the size of the food particles prepared by koalas (Lanyon & Sanson, 1986b), whereby the stomachs of animals with very worn teeth had much larger particles and a greater proportion of large particles than did animals with unworn teeth. Similarly, Gipps & Sanson (1984) found that ringtail possums *Pseudocheirus peregrinus* with higher levels of tooth wear had significantly lower digestibilities than animals with less worn teeth. Perhaps more important, however, was Pahl's (1987) illustration of how increased rates of tooth wear in populations of ringtail possums translated into lower adult survival and an apparent decrease in fecundity. Hence, tooth wear has the potential to impose severe limitations on the behaviour, physiology and longevity of an animal.

To offset the effects of reduced masticatory effectiveness, and therefore maintain energy balance despite tooth wear, energy intake must presumably be maintained through some compensatory mechanisms. Perez-Barberia & Gordon (1998b), found that female red deer *Cervus elaphus* partially compensated for reduced molar effectiveness by modifying food intake and investing more time and energy in chewing. Furthermore, although Lanyon & Sanson (1986b) found that tooth wear did affect the size of the food particles present in the small intestine of koalas, such consequences were

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only apparent under conditions of extreme wear. This suggests that koalas are able to compensate for the alteration in masticatory effectiveness associated with tooth wear and that, up to a point, the degree of compensation increases as the teeth become increasingly more worn. Hence, the aim of this study was to investigate how the feeding behaviour of koalas is altered so as to compensate for the effects of tooth wear.

METHODS

Study site

The 25-ha study site was located in coastal manna gum woodland on the south-west side of Raymond Island, c. 300 km east of Melbourne, Australia (38°55'S, 147°45'E). The low, open vegetation was dominated by coastal manna gum *Eucalyptus pryoriana* with a thick understory of bracken fern *Pteridium esculentum*, the former representing a dietary monoculture with respect to known koala food tree species. Koalas have successfully colonized the manna gum woodlands of Raymond Island since the introduction of a founding population of 32 individuals in 1953. The investigation took place in April 1999, in which the average minimum and maximum temperatures were 7.4 °C and 19.5 °C, respectively. This site and time combination was selected, as they provided a situation where only mature foliage of a single food tree species was available, thus preventing dietary differences from having an influence on the intake and chewing behaviours (e.g. Gross *et al.*, 1995) of individual koalas.

Field methodology

Five male koalas *Phascolarctos cinereus* of varying degrees of tooth wear, were captured using the methods described by Lee & Martin (1988). Tooth wear was calculated based on the descriptions of Martin (1981). Hence, tooth wear represented a continuous scale potentially ranging from 0 (unworn) to 7 (completely worn or absent). Upon capture, each animal was weighed (± 100 g), assessed for the degree of tooth wear and fitted with a collar containing an acoustically sensitive audio transmitter (Greager, Jenness & Ward, 1979; Lentle, Potter *et al.*, 1998). Microphone transmissions were initially monitored using a Uniden Bearcat (66–512 MHz, 1k) scanner and hand-held Yagi antenna. This equipment was also used to locate individuals by orientating towards the direction of greatest field strength. Animals were released within 10 min of capture, and their recovery and well-being periodically monitored for 72 h thereafter. During this time, the various sounds transmitted by the collar were calibrated against koala behavioural activities. Thereafter, each individual was randomly allocated to 2 of the next 12 days, during which the sounds that it made over a continuous 24-h period (beginning at 16:00) were recorded. Watson &

Dawson (1993) and Lentle, Potter *et al.* (1998) highlighted the influence of weather conditions on the feeding behaviour of free-ranging herbivores. Hence, daily (24 h) recording sessions that contained either rain or high winds were abandoned and postponed for an additional day.

The microphone transmissions were recorded onto 3 sequential, 5-h stereo HiFi BASF videocassette tapes, using a long play, Panasonic stereo HiFi VCR via a Uniden Bearcat (66–512 MHz, 1k) scanner attached to a Discone wide band, omni-directional antenna raised to 5 m. The VCR and scanner were powered by 1 of 3 Century 86T deep cycle batteries in a charge/discharge rotational cycle, via a 140-W inverter. A concurrent video time stamp was provided by an IR CCD camera focused on a small stopwatch.

At the conclusion of the experiment, individuals were recaptured, weighed and the collar removed. The dentition was also re-examined. All individuals had either maintained or slightly gained weight over the 18 days.

Laboratory methods

The tapes were played back in real time through an AV monitor that was capable of displaying the video time signal and amplifying the audio signal. In-house software (written by ML), synchronized to the playback, permitted each audibly recognizable event (such as a chew) to be digitally flagged, along with the exact time and date at which the event occurred.

The resulting digital data were subsequently manipulated to calculate the following feeding parameters per animal per day (24 h): number of leaves consumed; time spent feeding; chews per bite; total number of chews; chew rate; leaf consumption rate. Observations indicated that koalas ingested only 1 leaf at a time. Hence, the total number of leaves consumed per animal per 24 h was calculated as the number of biting (excising) sounds detected. The total number of chews per animal per 24 h was calculated as the number of chewing sounds detected for that time period. The number of chews per leaf was calculated by dividing the number of biting sounds per animal per day by the total number of chews for that period. Each of these feeding performance parameters was subsequently expressed as an average for the 2 24-h recording sessions for each animal.

Chewing rates were determined by first calculating the time (ms) elapsed between 2 consecutive chewing events. The chewing rate for each 24-h session was then calculated as the average of each of the individual inter-chew intervals over that period, excluding those intervals exceeding 5000 ms. These rates were then converted into the number of chews per s by dividing 1 by the average intervals. Finally, the average chew rate (chews s^{-1}) per animal per 24 h was calculated. Leaf consumption time was defined as the time (s) that elapsed between 2 consecutive bite events that were not > 60 s apart. The

average leaf consumption time was then calculated for each individual per 24 h.

Data analysis

Linear regression analyses were calculated to determine the effect of increased tooth wear on the mean time spent feeding (h) per 24 h, mean number of chews per 24 h, mean number of leaves consumed per 24 h, mean chew rate (chews s^{-1}) per 24 h, and the number of chews per bite per 24 h. All parameters were scaled for metabolic weight. All statistical analyses were carried out using SYSTAT (Wilkinson, 1990).

RESULTS

An increase in tooth wear was found to be associated with a significant increase in the mean number of leaves consumed per 24 h ($P=0.009$), mean time spent feeding per 24 h ($P=0.008$), mean number of chews per leaf per 24 h ($P=0.002$), mean number of chews per 24 h ($P<0.001$) and mean chew rate per 24 h ($P=0.016$) (see Fig. 1a–e). Despite this increase in chew rate, the increased number of chews per leaf resulted in a significant decrease in mean leaf consumption rate (leaves min^{-1}) per 24 h ($P=0.027$) (see Fig. 1f). The individual with the highest degree of tooth wear was found per 24 h to consume 41% more leaves, spend nearly 62% more time feeding, chew each leaf 25% more, perform 116% more chews, chew at a 15% higher rate and consume leaves 25% slower than the adult with the lowest degree of tooth wear.

DISCUSSION

Mastication is the primary factor determining the rate and extent of fermentation (Pearce & Moir, 1964). Consequently, by jeopardizing the degree to which food material is processed, reduced masticatory effectiveness has the potential to reduce both the rate and extent of nutrient and energy uptake. Perez-Barberia & Gordon (1998a) considered three potential mechanisms by which herbivores could compensate for reduced masticatory effectiveness: (1) increasing the chewing effort per unit of food processed; (2) altering the voluntary intake and passage rate; (3) selecting food items that are more easily processed. Ultimately, the role of these mechanisms is to maintain a fill of fine particles within the fermentation chamber(s) of the gut.

Dietary shifts in response to tooth wear were not tested in the present study. Different foliages are likely to require different feeding strategies in order to achieve the same nutritional outcome. Indeed forage differences have been found to have a significant effect on the feeding performance of Nubian ibex (Gross *et al.*, 1995) and free-ranging tammar wallabies *Macropus eugenii* (Lentle, Stafford *et al.*, 1999). Consequently,

altered food preferences could potentially interact with, and obscure the effects of tooth wear on, food intake and chewing performance. Hence, a site was selected that had only one food tree species and mature foliage available so as to minimize compounding factors.

Intake modification

Increased tooth wear was found to be associated with a 41% increase in the number of leaves consumed from 681 to 963 per day (24 h). Put into perspective, this is substantially higher than the increases in intake attributed to the effects of seasonal variations, foliage age and foliage composition (Ellis *et al.*, 1995; Hume, Bladon & Soran, 1996; Lawler *et al.*, 1998), all of which are considered to be of biological significance. Lanyon & Sanson (1986b) found that with increased tooth wear, the proportion of fine particles produced by mastication decreased, but that this is not reflected by the size of particles retained in the caecum. This is facilitated by the selective retention of fine particles within the caecum/proximal colon relative to the larger, less digestible particles that pass through more quickly (Cork & Warner, 1983), thereby reducing the gut filling effect.

Worn teeth produce a smaller proportion of fine particles Lanyon & Sanson (1986b). However, by increasing food intake and gut passage rate, as well as selectively retaining the fine particles, koalas might be able to maintain a caecum fill of fine particles, thereby partly compensating for tooth wear.

Conversely, in the only other investigation into compensatory mechanisms used to offset reduced masticatory effectiveness, Perez-Barberia & Gordon (1998b) found that red deer *Cervus elaphus* with low occlusal effectiveness had lower voluntary intakes than deer with higher effectiveness. This disparity is likely to be the result of major differences in digestive strategies between foregut fermenters and hindgut fermenters. Whilst small particles and solutes are selectively retained in the hindguts of some hindgut fermenters, such as koalas (Cork & Warner, 1983), greater gliders *Petauroides volans* (Foley & Hume, 1987) and rabbits (Bjornhag, 1972), it is the larger particles (> 1 mm) that are retained in the rumen of ruminants (Campling & Freer, 1962; Balch & Campling, 1965). Consequently, in ruminants, a reduction in masticatory effectiveness may lead to an increase in retention time, and thus a decrease in gut passage rate and voluntary intake. Although Perez-Barberia & Gordon (1998b) did not detect a corresponding decrease in retention time, they acknowledged that the techniques used to measure retention time may have been inadequate.

Associated with the need to increase food intake, there was a 62% increase in the amount of time invested in food procurement. Nagy & Martin (1985) found that free-ranging koalas spend *c.* 80% of the time resting or sleeping. Such large periods of inactivity are believed to enable koalas to maintain relatively low energy require-

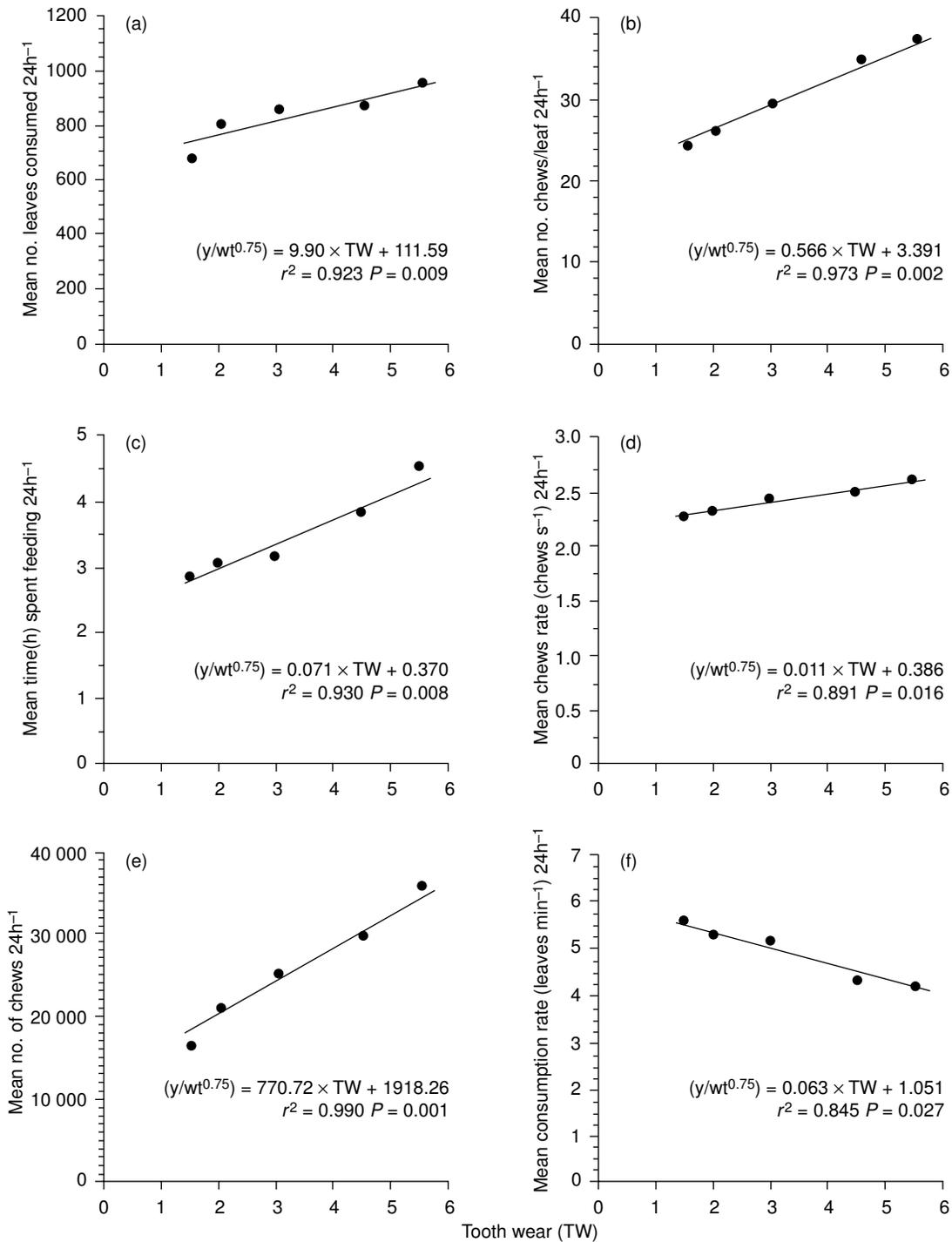


Fig. 1. Linear regression of various feeding parameters against tooth wear ($n = 5$) in male koalas *Phascolarctos cinereus*: (a) mean number of leaves consumed per 24 h; (b) mean number of chews per leaf per 24 h; (c) mean time (h) spent feeding per 24h; (d) mean number of chews per 24 h; (e) mean chew rate (chews s^{-1}) per 24 h; (f) mean consumption rate (leaves min^{-1}) per 24 h. Corresponding equations, r^2 and P -values for linear regression analysis of tooth wear against each feeding parameter scaled for metabolic weight are given ($n = 5$). Each point represents the average of two separate, continuous 24-h recording sessions for a single individual.

ments, and thus to use a poor quality diet (Cork & Sanson, 1990). Therefore, a 62% increase in the amount of time spent feeding per day is likely to impose significant limitations on overall time budgeting and energetics.

Chewing behaviour

The rate at which koalas chew was also found to increase significantly with increasing tooth wear, suggesting that food processing ability can be at least partly

maintained by increasing the rate of occlusion. Potentially a blunter shearing blade might be more energetically efficient at faster chew rates, whilst a sharper blade might be more energetically efficient at a slightly slower rate. Domingue, Dellow & Barry (1991), attributed the differences in chewing effectiveness between goats and sheep to differences in the rate at which they chew. Increasing the rate at which plant material is sheared by the teeth may alter the way that the material fractures. Aranwela, Sanson & Read (1999) found that the force required to fracture leaf material, decreased with increased shearing velocity. Hence effectively different shearing blades may produce similar shearing results when occluded at different rates. Increased chew rates may also generate higher bite forces, thereby resulting in higher chewing efficiencies (Julien *et al.*, 1996). Alternatively, an increase in chewing rate may serve to reduce the amount of time required to consume the increased quantity of food material necessary to compensate for increased tooth wear.

Koalas were shown to compensate for tooth wear by increasing the number of chews per leaf. At the time of this investigation, only mature leaves of similar size were available, and koalas were observed to incise only one leaf at a time. Therefore, an increase in the number of chews per leaf, directly equates to an increase in the number of chews per unit of food material. In humans, the number of chews per mouthful of food is the principal determinant of median particle size (Voon *et al.*, 1986), whereby an increase in chewing effort shifts the distribution of particle sizes further towards the smaller particles. Hence, Perez-Barberia & Gordon (1998b) suggested that increasing the number of chews per unit of processed food material enables the distribution of ingesta particle sizes to be maintained as the teeth become less effective.

Combined with an increase in leaf intake, the greater number of chews per leaf resulted in a substantial (116%) increase in the average number of daily chews. This further emphasizes the increase in feeding investment that is necessary to maintain energy intake as the teeth become more worn.

Despite having a faster chew rate, the increased number of chews per bite resulted in a strong negative relationship between tooth wear and bite rate. Lanyon & Sanson (1986a) illustrated the ratchet-like manner in which leaves are moved across the cheek teeth at a steady rate of one molar row width per occlusal 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. It is suggested here that the newly cut edge of the leaf is dragged posterolabially onto the labial cones of the upper molars at a rate that is dependent on the sharpness of the cones. Sharp, unworn teeth might therefore feed more leaf material into the mouth per stroke than old, worn teeth. Consequently, by determining the rate at which a leaf is fed across the

masticatory apparatus, the teeth themselves might be directly responsible for controlling the number of chews per leaf. Therefore, as wear reduces the effectiveness of the teeth, the altered dental morphology modifies the intake rate such that less leaf material is masticated per occlusal stroke.

According to Lanyon & Sanson (1986b), the masticatory effectiveness (as measured by the length of the cutting edges) of koala teeth initially increases as tooth wear advances. This is brought about by an overall increase in the length of the cutting edges of the occlusal surfaces. Eventually however, further reductions in the occlusal surface area, rapidly reduce the length of the tooth's cutting edge, and thus reduce its food processing effectiveness. However, the current findings indicate that molar effectiveness decreases continually with increasing tooth wear, and therefore, is not necessarily determined by cutting edge alone.

Ecological significance of tooth wear

Tooth wear compensations, particularly with respect to extra time and energy investiture, must come at the expense of other activities. Hence, substantial increases in feeding investment caused by advancing tooth wear are likely to impact severely on the animal's overall time and energy budgeting. In turn, reduced time and energy availability could affect the individual's social capabilities and thus reproductive output.

Ultimately, by affecting one of the major means of nutrient acquisition, tooth wear has the real potential to define longevity within koala populations. Once the teeth reach an advanced stage of wear, they are incapable of processing food material adequately. Compensations can only work up to a point, and once ineffective, the animal starves with a gut full of large particles. Consequently, individuals within populations that consume a more abrasive diet will have faster rates of tooth wear and reduced longevity.

The compensation mechanisms described here and elsewhere (Perez-Barberia & Gordon, 1998b) are not unique to dealing with reduced masticatory effectiveness. Gross *et al.* (1995) found that Nubian ibex compensated for food particle size and sex-related differences in body size by increasing chewing investment (chews/g). Weston (1988) found that lactating ewes consumed more and ate more rapidly than non-lactating ewes. Lactation is an energetically demanding process that necessitates substantial increases in energy requirements (Gittleman & Thompson, 1988; Cork, 1991). Koalas carry very little fat reserve (Degabriele, Harrop & Dawson, 1978; Ellis & Carrick, 1992), and therefore may increase intake and/or chewing effort in order to compensate for the increase in energy requirements associated with lactation. This is likely to become increasingly more significant with age. The female's potential to compensate for lactation will depend on the degree to which it is already compensating for tooth wear. The reproductive success of male koalas is also

likely to be linked to tooth wear. Increased tooth wear could lead to a reduction in the amount of time and energy available to defend resources, seek mates and interact with other individuals. Consequently, tooth wear could define not only the longevity of koalas, it could also determine reproductive longevity and thus fecundity.

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