

The effects of tooth wear on the activity patterns of free-ranging koalas (*Phascolarctos cinereus* Goldfuss)

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Abstract

The free-ranging activity patterns of five adult males and one sub-adult male koala (*Phascolarctos cinereus*) with varying degrees of tooth wear were investigated using acoustically sensitive radio-telemetry. Increased tooth wear was found to be associated with a significant decrease in the amount of time spent sleeping and being inactive. Furthermore, compared with individuals with low degrees of tooth wear, individuals with high tooth wear were found to spend considerably less time moving within and between trees, and had home ranges an order of magnitude smaller. Hence, feeding compensations were found to come at the expense of other activities such as sociality and therefore have important consequences for reproductive output. Individuals with high tooth wear also spent longer feeding per bout, and spaced feeding bouts out more evenly throughout a 24-h period, thereby exhibiting reduced degrees of nocturnality. The sub-adult was found to range over a disproportionately large area and spend a relatively large amount of time moving between trees, indicative of a dispersing individual. Moreover, the activity patterns of this individual were found to differ slightly from the adult trends and were perhaps affected by the extra energetic demands associated with dispersal.

Introduction

Koalas are arboreal folivores that feed almost exclusively on the leaves of *Eucalyptus* trees, which are low in protein, are physically difficult to process, are highly defended chemically and at times toxic (Cork and Sanson 1990). Part of the chemical defense involves reducing the availability of protein, thereby resulting in a low-nutrient diet that is further diluted by large amounts of relatively indigestible plant cell wall (fibre). Koalas are hindgut fermenters and therefore, in order for them to digest this high-fibre diet, the food material must first be broken down finely by the teeth.

Whilst various aspects of the ecology of koalas (such as dietary selection and preference) have been studied extensively, the activity patterns of free-ranging koalas have received very little attention. However, preliminary studies have indicated considerable variation in the timing and duration of activities (Hindell *et al.* 1985; Nagy and Martin 1985) between individual koalas. Unfortunately, the sources of variation were neither explored nor discussed.

Mastication is the primary factor determining the rate and extent of fermentation in herbivores (Pearce and Moir 1964). Whilst, initially, koala molars have high, tightly interlocking cusps with opposing long, curved blades (Lanyon and Sanson 1986a), the occlusal action and the abrasiveness of the leaf material cause the teeth to wear down (Lanyon and Sanson 1986b). Consequently, by jeopardising 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. In order to maintain energy intake despite tooth wear, free-ranging koalas have been found to increase food intake, spend more time feeding, and enhance chewing effort (Logan and Sanson 2002a). However, this increase in feeding investment is likely to come at the expense of other activities. Individuals with high

degrees of tooth wear that spend more time feeding, may have less time and energy available to devote to other activities such as resource protection and social interactions. Consequently, tooth wear may also have the potential to impose severe limitations on the time budgeting and home ranges of free-ranging koalas.

The aim of this study was to investigate the consequences of increasing tooth wear on the time budgeting and home ranges of free-ranging koalas for which feeding consequences were being concurrently measured (Logan and Sanson 2002a).

Methods

The study was carried out in April 1999 within a 25-ha coastal manna gum woodland site on the south-western side of Raymond Island (off Paynesville, 300 km east of Melbourne, Australia) in conjunction with an investigation into the patterns of tooth wear on the feeding behavior of free-ranging koalas (see Logan and Sanson 2002a). This site and time combination was selected to ensure that only mature foliage of a single food tree species (*Eucalyptus viminalis pryoriana*) was available, thereby preventing dietary differences from having an influence on nutritional intake (Gross *et al.* 1995) of individual koalas.

One sub-adult and five adult male koalas of varying degrees of tooth wear were captured from a wild population on Raymond Island. Each koala was weighed (to ± 100 g), assessed for degree of tooth wear, and fitted with a transmitter collar containing an acoustically sensitive audio transmitter (Greager *et al.* 1979; Lentle *et al.* 1998a; Logan and Sanson 2002a), before being released back into the tree from which it had been captured. The 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 were of good body condition. Tooth wear followed Martin (1981) and was further confirmed using the descriptions of Lanyon and Sanson (1986b) and Gordon (1991). When premolar wear features were between the classes described by Martin (1981), fractional scores depicting the degree of deviation from each class were used (e.g. Wear Class 4.5 had features between Classes 4 and 5). Hence, tooth wear represented a scale potentially ranging from 0.0 (unworn) to 7.0 (completely worn or absent). It should be noted that whilst tooth wear is often used with varying degrees of success to estimate the age class of animals (Gipson *et al.* 2000), in the current study tooth wear was investigated for its potential to reduce energy and nutrient intake rather than to act as a surrogate for age determination.

Animals were released within 10 min of capture, and their recovery and well-being periodically were monitored for 72 h thereafter. During this time, the various sounds transmitted by the collars were calibrated against koala behavioural activities. Thereafter, each individual was randomly allocated to two of the next 12 days, during which all the sounds detected and transmitted by its collar over a continuous 24-hr period (commencing at 16:00 hours) were recorded onto the audio channel of three sequential, 5-h stereo HiFi BASF video-cassette tapes (to enable extensive recording periods, up to 10 h), using a long-play Panasonic stereo HiFi VCR via a Uniden Bearcat (66–512 MHz, 1k) scanner attached to a Discone wide-band, omnidirectional antenna raised to 5 m. A concurrent video time stamp was provided by an IR CCD camera focussed on a small stopwatch. The VCR, camera and scanner were powered by one of three Century 86T deep-cycle batteries in a charge/discharge rotational cycle, via a 140-W inverter.

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

Time budgeting

VCR tapes were later replayed in real time and in synchrony with event-recording software (written by M. Logan). Each audibly recognisable event was thereby digitally flagged along with the exact time and date at which it had occurred. Events were divided into five activity categories: feeding (chewing, biting and other food-procurement sounds), moving within a tree (climbing sounds), walking on the ground between trees (walking, running sounds), resting (defined by the presence of regular wakeful sounds such as head/limb movements, scratching, vocalising) and sleeping (defined by the presence of breathing sounds and absence of all other major wakeful sounds for a period of at least 5 min). An additional category, 'inactive', which combined resting and sleeping, was subsequently added. For each minute, the audible event(s) along with corresponding activity category was recorded, so as to calculate the amount of time spent sleeping, feeding, etc per 24 h. In the event that two or more categories co-occurred, the category recorded was determined on the basis of a rarity hierarchy (walking–moving–feeding–inactive–sleeping), where walking was the rarest and was given highest priority. A feeding bout was defined as a continuous

block of feeding sounds that were not interrupted by more than 5 min of either resting or sleeping sounds, and thus the lengths of feeding bouts and inter-feeding bouts were calculated as the number of minutes elapsed within and between each feeding bout respectively for each 24-h period. A 5-min cut-off for defining both feeding bouts and sleeping activity patterns was selected after preliminary video observations and sound calibrations for each individual found that 100% of such activity categories could be correctly recognised from such a protocol, whilst shorter periods led to incorrect identifications. These activities were then expressed as the average amounts of time (h) spent per 24 h for each of the two separate, yet continuous 24-h recording sessions for each individual. The amounts of time spent moving and walking were calculated as the amount of time (s) that elapsed for each moving and walking event respectively. These activities were then expressed as the average amount of time (min) spent per 24 h for each of the two separate, yet continuous, 24-h recording sessions for each individual. The timing and duration of social interactions and bellows were also noted.

Home range

Home-range analyses that are based on statistical methods (such as probabilistic and, to a lesser degree, harmonic mean and cluster analysis) usually assume that each successive 'fix' is independent (Swihart and Slade 1985). Of particular concern are the situations in which fixes that are closer together in time are also closer together in space (temporally autocorrelated). Although rarely tested (Harris *et al.* 1990), the more strongly autocorrelated the data is, the more severely these techniques will tend to under-estimate the true size of the home range (Swihart and Slade 1985). Consequently, Harris *et al.* (1990) recommended that temporally autocorrelated data should be analysed using simple polygon home-range methods. Despite showing a slight tendency to seek out shade during the heat of the day (M. Logan, unpublished data), koalas do not return to a single location (such as a den or tree hollow) on a daily basis. Consequently, daily location fixes for koalas are expected to be temporally autocorrelated.

Throughout the recording period, the one sub-adult and five adult koalas were routinely located by orientating a hand-held Yagi antennae towards the direction of greatest signal strength, and progressively de-tuning a Uniden Bearcat (66–512 MHz, 1 k) scanning receiver on approach. All individuals were located once per day between 08:00 and 09:00 hours for a total of 22 consecutive days for home-range analysis. Animal locations were determined by estimating the position (to ± 5 m) within a 1000 m \times 1000 m reference grid with 50-m increments. To determine the degree of tree sharing, individuals were also relocated when the sound signals indicated a change in tree.

Data analysis

Linear regression analyses were performed to determine the effect of increased tooth wear on the mean amount of time spent on each activity per 24-h period, per day (sunrise to sunset) and per night (sunset to sunrise). The sub-adult was expected to have different energy and ranging requirements than the adults as it was still growing and dispersing. This was considered likely to have an effect on its overall activity patterns, and therefore, it was excluded from tooth-wear regression analyses and hereafter is discussed only as datum relative to the adult trends. Paired *t*-tests were used to examine the temporal distributions of activity patterns in relation to photoperiod. Regressions and *t*-tests were carried out using SYSTAT (Wilkinson 1990). Temporal autocorrelations of home-range data were confirmed using Mantel tests (Legendre and Fortin 1989) and home ranges were subsequently calculated using 95% minimum convex polygons (CALHOME software: Kie *et al.* 1994). Incremental area analysis confirmed that the number of fixes (22) was adequate to describe the home ranges of each of the adult koalas. However, the range estimates of the sub-adult were likely to be underestimated.

Results

Time budgeting

When data for each individual were averaged across days, adult male koalas were found to spend 12.5–13.5 h sleeping, 6.01–6.6 h resting, 2.84–4.6 h feeding, 6.86–46.7 min moving, and 0.37–4.81 min walking per 24-h period. Associated with an increase in tooth wear, there was a significant decrease in the average number of hours spent sleeping per 24-h period (Fig. 1a). Furthermore, the data suggested that the time spent sleeping during the day decreased with increased tooth wear, whilst it increased during the night (Fig. 1a); however, these trends were not significant. Although increasing tooth wear was not found to affect

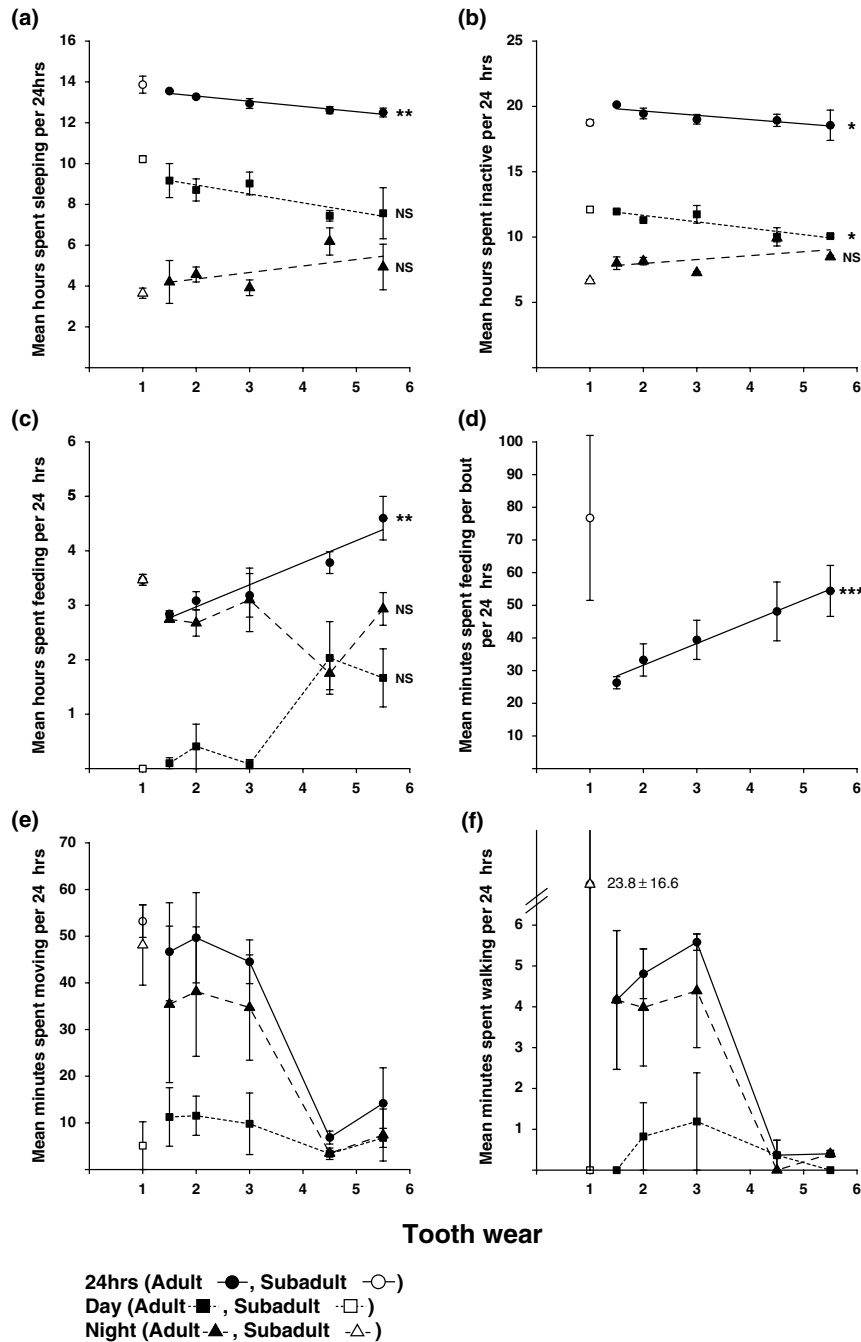


Fig. 1. The effect of tooth wear on the average amount of time spent (a) sleeping, (b) inactive, (c) feeding, (d) feeding per bout, (e) moving within trees, and (f) walking between trees per 24-h period, day and night for male koalas (*Phascolarctos cinereus*). Each point represents the mean of two separate, yet continuous, 24-h recording sessions for a single individual. Note that the sub-adult was excluded from regression analyses. Statistical significance of relationships is indicated thus: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; or NS, $P > 0.05$.

the amount of time spent resting per 24-h period, day or night, tooth wear was found to be associated with a significant decrease in the amount of time spent inactive (sleeping and resting combined) (Fig. 1*b*). Again, the data suggest that increased tooth wear is associated with a decrease in time spent inactive during the day (Fig. 1*b*) and a slight increase during the night (Fig. 1*b*), although the latter trend was not significant.

Associated with an increase in tooth wear, there was a significant increase in the amount of time spent feeding per 24-h period (Fig. 1*c*). Interestingly, this trend was not found in the amount of time spent feeding during the day or night (Fig. 1*c*). The two individuals with high degrees of tooth wear showed a shift towards spending as much time feeding during the day as the night. The average length of feeding bouts (Fig. 1*d*) and inter-feeding bouts were also found to increase significantly with increasing tooth wear ($b = 36.753$, $t = 3.633$, $P = 0.036$).

Neither the amount of time spent moving, nor the amount of time spent walking were found to be linearly affected by tooth wear (Fig. 1*e-f*). However, Fig. 1*e-f* shows that whilst initial increases in tooth wear were not associated with an increase in the amount of time spent moving and walking, more advanced degrees of tooth wear corresponded to a dramatic decline in both moving and walking.

Fig. 2 demonstrates the variability in duration and timing of activities throughout the 24-h period for the two separate, yet continuous, 24-h recording sessions for each koala. Despite the large degree of daily variation in activity timing between the two days within an individual, Fig. 1*a-f* shows that the duration of the major activities are highly consistent between the two days and that variations in duration between individuals can be well explained (sleeping, $R = 0.955$; inactivity, $R = 0.855$; feeding, $R = 0.930$) by degree of tooth wear. Fig. 2 also illustrates that, while the activity patterns of individuals with low-to-medium tooth wear are mainly 'nocturnal', the activity patterns of the two individuals with high tooth wear approach a pattern whereby they are active during the day and night.

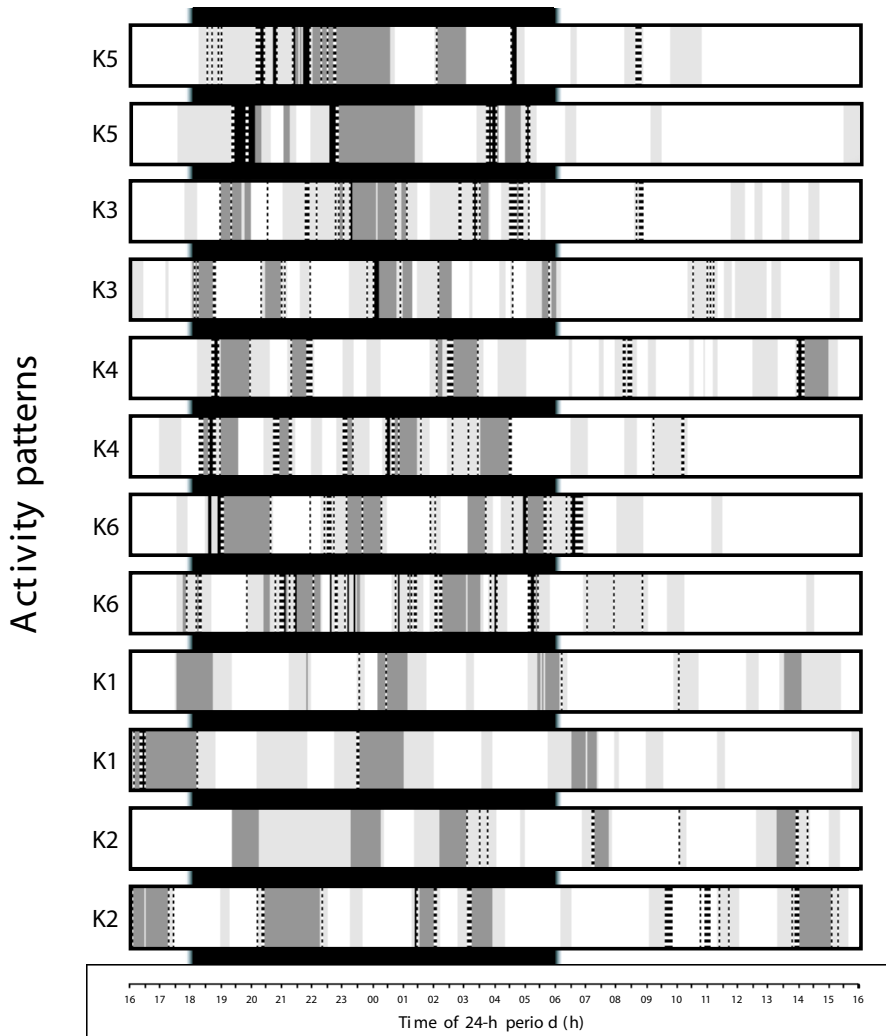
The activity durations of the sub-adult male koala were found to resemble those of individuals with medium-to-high tooth wear. The sub-adult individual was found to spend less time inactive and more time feeding than the adult koalas with low tooth wear, and, in so doing, with respect to feeding and inactivity, resembled individuals with medium or high degrees of tooth wear.

Nocturnality

Overall, koalas were found to spend significantly more time resting, feeding and moving during the night than during the day, and significantly more time during the day sleeping and inactive (Table 1). Interestingly, these relationships are weaker for the two individuals with high degrees of tooth wear. In addition, Fig. 1*e* suggests that the koalas spend more time walking during the night than day, although this trend is reversed for the two high-tooth-wear individuals, leading to an overall non-significant result.

Home range

Not surprisingly, the relationship between home-range size (Fig. 3) and tooth wear was similar to that of time spent walking and tooth wear (Fig. 1*f*). Initial increases in tooth wear were not associated with any major changes in home range; however, further increases in tooth wear corresponded to a substantial decrease in home range. The home ranges of adult male koalas with high tooth wear were one-tenth the size of the ranges of adults with low-to-medium tooth wear (Fig. 3). Furthermore, the home-range size of the sub-adult male koala was ten times larger than those of the adults with low-to-medium tooth wear.



Activity categories

- sleeping
- resting
- feeding
- moving within trees
- walking between trees

Fig. 2. Duration and distribution of daily activities of one sub-adult and five adult male koalas monitored remotely for two separate, yet continuous, 24-h recording sessions from a free-ranging population on Raymond Island (Victoria, Australia). Individuals K5 through to K2 represent an increase in tooth wear.

Discussion

Time budgeting and home range

Logan and Sanson (2002a) found that adult male koalas compensated for increasing tooth wear by increasing feeding effort. In particular, increased tooth wear was associated with a

Table 1. Summary of paired *t*-tests comparing the amount of time spent engaged in various activities during the night versus the day
The sub-adult is included, hence $n = 6$ and d.f. = 5. Bold type indicates significant ($P < 0.05$) relationships

Activity	<i>t</i>	<i>P</i>
Resting	11.359	<0.001
Sleeping	-4.940	0.004
Inactive	-3.906	0.011
Feeding	3.686	0.014
Moving	2.928	0.033
Walking	1.553	0.181

significant increase in the amount of time spent feeding per 24-h period, which was in turn attributed to a significant increase in food consumption and number of chews per unit of food material. Logan and Sanson (2002a) also suggested that these compensations are likely to occur at the expense of other activities.

In the present study, increased tooth wear was associated with a significant decrease in the mean number of hours spent sleeping and inactive per 24-h period (Table 1, Fig. 1a–b). This represents a 7.85% decrease in daily inactivity from 20.14 h (83.92%) to 18.56 h (77.33%) per 24-h period. These values are similar to the estimates of inactivity of free-ranging koalas of 80.4% (Nagy and Martin 1985) and 85% (Mitchell 1990a), as well as inactivity data on sloths (83%: Beebe 1926), another arboreal mammal that consumes a high-fibre diet. Whilst assimilation of a high-fibre diet usually necessitates a large body size (>20 kg) to enable a large gut capacity relative to metabolic energy requirements (Demment and Van Soest 1985), arboreality inhibits this allometric relationship. Thus, it has been suggested that the low levels of activity exhibited by arboreal folivores, as well as low metabolic rates (Nagy and Montgomery 1980; Nagy and Martin 1985), enable them to conserve energy (McNab 1978) and therefore to maintain a high-fibre diet. Logan and Sanson (2002) speculated that the increased time and effort invested in compensating for

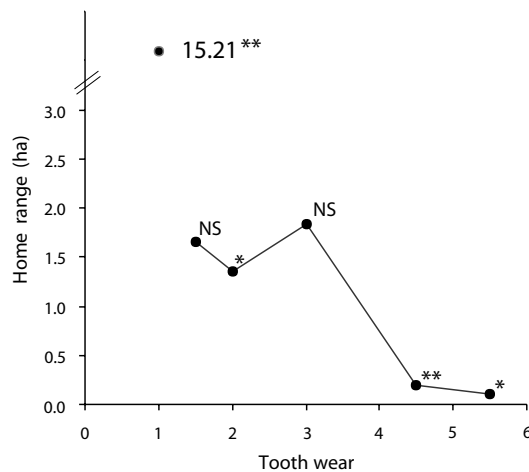


Fig. 3. The effect of tooth wear on the home range (ha) of one sub-adult and five adult male koalas (*Phascolarctos cinereus*). Ranges were calculated as 95% minimum convex polygons to avoid the problems associated with the temporally autocorrelated data. Significance levels of Mantel *R* values are indicated thus: *, $P < 0.05$; **, $P < 0.01$; or NS, $P > 0.05$.

increasing tooth wear were likely to equate to an increase in the overall energy investment in feeding. A 7.85% decrease in daily inactivity may lead to a substantial decrease in energy conservation, thereby further reducing the energy available for other activities.

The associations of tooth wear with the amount of time spent moving, the amount of time spent walking and the home-range size all produced similar trends. Whilst initial increases in adult tooth wear were not found to correspond with any obvious changes in either moving, walking or range size, individuals with more advanced tooth wear spent substantially less time moving and walking, and had range sizes an order of magnitude smaller. Koalas typically inhabit open eucalypt forests and woodlands that have little or no continuity between tree canopies, and if contact between trees exists, it is only by branches that are too thin to support a koalas' weight (5–12 kg). Therefore, unlike many other arboreal folivores that are either smaller, or else inhabit more continuous canopies, the only means by which a koala can travel between trees is to walk along the ground. Compared with sleeping, resting and perhaps even feeding, traveling between trees is likely to be an energetically expensive activity, particularly when the koalas' presumed delicate energy balance is considered. Although koalas move between trees for a number of reasons, they presumably do so primarily for food, shelter and resource protection, and when engaging in (or avoiding) social interactions. Similarly, koalas move within a tree for a number of reasons, including access to leaves, access to a more secure or shaded roost, scent marking, and to engage in (or avoid) antagonistic social interactions. Therefore, a reduction in the amount of time spent walking and moving, and in the size of the home range, suggests either a reduction in sociability and/or a reduction in other non-maintenance and more dispensable activities. It should also be noted that the current study took place in the non-breeding season, where interactions might be expected to be less frequent than in the breeding season. Consequently, the above patterns may be even more pronounced in the breeding season.

Throughout the duration of the field investigation, the two high-tooth-wear individuals were observed to utilise a relatively small number of trees, often spending two or three days at a time in the one tree. Furthermore, despite being in close proximity to many other adult male koalas, these individuals did not engage in any social behaviors such as scent marking and vocalisation, which are thought to advertise an individuals' range to its neighbours (Mitchell 1990b). Furthermore, these two individuals rarely moved within a tree for the purpose of returning to a more secure or shaded roost after feeding. Instead, they tended to sleep and/or rest within the clump of leaves from which they had been feeding. The absence of ranging behaviour, along with the small distances moved per day and the low number of trees used, suggests that these individuals ranged purely for the purpose of obtaining fresh leaves, rather than to maintain a social position. In fact, Logan and Sanson (2002b) found that these individuals displayed considerably less sociability than individuals with low-to-medium tooth wear. Hence advanced tooth wear may, by reducing the amount of time and energy available for non-maintenance activities, lead to a reduction in the social involvement and, potentially, the reproductive output of male koalas.

Mitchell (1990a) also found that the home ranges of male koalas varied considerably between individuals, ranging from <0.5 ha to >3.5 ha. Furthermore, koalas older than 4 years appeared to be the most variable; some of these individuals had the smallest home ranges and only rarely engaged in social behaviors such as bellowing, scent marking and interactions. Although the relationship between tooth wear and age for koalas consuming *Eucalyptus viminalis* is unknown, a study conducted on a Queensland population (Gordon 1991) suggests that animals four years and older are likely to be of Tooth Wear Stages 2 and higher. Therefore, koalas that are older than 4 years are likely to exhibit degrees of tooth

wear ranging from low to very high, which may, in turn, account for at least some of variability in ranging and sociality of this group.

The sub-adult male spent considerably more time walking per 24-h period, and had a much larger home range, than did the adult koalas. Unlike the adults, the sub-adult did not have an established range, and was repeatedly attacked and pursued by resident adult males. Often, it would begin to scale a tree, only to return promptly to the ground and continue walking. While this was sometimes due to the presence of another koala, on other occasions there were no obvious audible reasons why the animal had rejected that tree. One explanation is that the sub-adult had detected the recent presence of another koala and moved on in an attempt to avoid a confrontation. It was also noted that while this animal did range into the ranges of all the other collared individuals, it did not use any of the trees that they had visited over the time of the investigation. The movement patterns of this individual were thus more consistent with a dispersal event than with typical ranging behaviour, hence the relatively large range size.

Previous studies (Nagy and Martin 1985; Hindell *et al.* 1985; Mitchell 1989) have noted considerable variability in the amount of time that free-ranging koalas allocated to various activities as well as the distribution of these activities throughout a 24-h period. Unfortunately, the sources of this variability were beyond the scope of these investigations, and thus were not explored. Slater (1981) suggested that most behavioural differences between individuals within a population are the result of differences in either size, gender and/or age. The present study also found substantial variability in both the timing and duration of activity patterns between individuals (Fig. 2). There also appeared to be a lack of activity pattern synchrony between days within individuals. Furthermore, as illustrated in Fig. 1a–c, the diurnal and nocturnal activity allocations within individuals were also highly variable. Despite the lack of synchronicity, however, individual koalas allocated very consistent amounts of time to sleeping, inactivity and feeding on a daily basis (Fig. 1a–c), and the associations of each with tooth wear explained 95.5%, 85.5% and 93.0% of the variability between individuals respectively. Potentially, then, at least some of the variability noted by Nagy and Martin (1985), Hindell *et al.* (1985) and Mitchell (1989) might have also been explained by differences in the degree of tooth wear between individuals.

Nocturnality

With few exceptions (numbat, *Myrmecobius fasciatus*; musky rat-kangaroo, *Hypsiprymnodon moschatus*; dusky antechinus, *Antechinus swainsonii*: see Strahan 1995), all extant marsupials are considered to be broadly 'nocturnal' in habit. Of these, the activity patterns of some such as the grazing macropodines, are considered to be 'crepuscular' (Lentle *et al.* 1998b), having activity peaks that coincide with the rising and setting of the sun. Others, such as certain dasyurids (e.g. *Antechinus stuartii* and *A. agilis*), are also considered to exhibit mildly 'polycyclic' rhythms, having elevated levels of daytime activity during various times of the year depending on energy/nutrient requirements (Koertner and Geiser 1995) and/or food availability (Dickman 1995). While koalas are considered to be nocturnal, the few studies that have investigated the activity patterns of koalas, are contradictory.

Nagy and Martin (1985) and Hindell *et al.* (1985) monitored the activity patterns of free-ranging koalas over continuous 24-h periods, and found that koalas fed at all times of the day, and that the amount of time spent sleeping during the day (63%) and night (60%) were not significantly different (Nagy and Martin 1985). Hence, Nagy and Martin (1985) concluded that the four female koalas studied, were not obviously 'nocturnal'. Conversely,

Mitchell (1989) estimated the long-term daily activity patterns of free-ranging koalas by calculating the average frequencies (percentage of instantaneous observations) of each activity over a punctuated 3.5-year period and found that koalas were clearly more active during the night than during the day. In particular, koalas were found to feed, travel and interact more at night than during the day, with the reverse trend for inactivity.

The nocturnal habit of koalas could be the result of phylogenetic constraints. However, for an animal that utilises a food source that is equally available throughout the entire 24-h period, 'nocturnality' does potentially offer an advantage as a means to avoid predation and/or extreme climatic conditions. Whilst the risk of predation on koalas is presently very low, predation by dingos (Kershaw 1906), aborigines (Coutts 1970), and, possibly earlier, by the marsupial lion (*Thylacoleo carnifex*), and the diurnal *Megalania* are thought to have been significant in the past. As koalas do not use any form of shelter other than foliage, they are also exposed to temperature extremes that can range from $<0^{\circ}\text{C}$ to $>40^{\circ}\text{C}$. The ability of koalas to endure cold weather is attributed to the high insulative properties of the pelt (Degabriele and Dawson 1979) and in postural modifications (Smith 1979). At the other extreme, koalas appear to endure hot weather only by sprawling across a branch and roosting in a shady tree. Consequently, koalas may experience greater difficulty coping with hot conditions than cold conditions. So nocturnality could enable the animal to avoid being active at a time that poses the greatest thermoregulatory stress.

Koalas spent significantly more time inactive, feeding, and moving during the night than during the day, and significantly more time during the day sleeping and being inactive (Table 1). However, as shown by Fig. 1, the differences in activities between day and night generally decrease with increasing tooth wear. These results suggest that while koalas do appear to be nocturnal, the degree of nocturnality may be forced to decrease with increasing tooth wear. Hence, again, differences in tooth wear might account for the differences in the distributions of activity patterns between individuals noted in Hindell *et al.* (1985). Fig. 2 shows that for koalas with low-to-medium tooth wear, most activity occurs between sunset and sunrise, whereas the two individuals with high tooth wear spaced activity more evenly throughout the entire 24-h period. Furthermore, increasing tooth wear was found to correspond to a significant increase in the amount of time spent feeding per feeding bout (Fig. 1*d*) as well as an increase in the time between feeding bouts per day. Therefore, koalas with advanced tooth wear may have been forced to feed for longer at a time, and to space feeding bouts out more regularly throughout the 24-h period. While individuals with low-to-medium tooth wear generally had shorter inter-feeding bouts, it should be noted that since these individuals did not usually feed between sunrise and sunset, the time between the last feed of one day and the first feed of the next day could be more than 12 h. Lanyon and Sanson (1986*b*) and Logan and Sanson (2002*a*) proposed that koalas partly compensate for increased tooth wear by increasing food intake and gut passage rate. To support an increased gut passage rate, while still maintaining high food quantities within the gut, it may be necessary not only to consume more food (Logan and Sanson 2002*a*) but also to space the feeding bouts out more regularly. This need may then ultimately dictate the diel distributions of other activity patterns. Therefore tooth wear may not only affect the feeding behaviour of free-ranging animals (Logan and Sanson 2002*a*), it may also have profound consequences for the timing and duration of all other activities, thus making it one of the most biologically important processes operating in natural herbivore populations.

It is acknowledged that this study is unable to uncouple the effects of tooth wear from other potential effects of pathological aging, and that, consequently, the patterns described may be the consequence of factors other than tooth wear. However, it is suggested that tooth

wear (and the associated effects thereof) is the major effect of aging in wild koalas. Tooth wear is known to be the primary cause of mortality and loss of condition in aged koalas from Raymond Island (Peter Mitchell, unpublished data). So while we acknowledge the above limitation, we believe that this study does provide an important stimulant for future research into the activity patterns of free-ranging koalas.

While tooth wear has been previously demonstrated to influence an animal's feeding ecology (Gross *et al.* 1995; Perez-Barberia and Gordon 1998), the consequences for other aspects of their behaviour, time budgeting and home ranges have previously received very little attention. In the present study, advanced tooth wear was found to be associated with substantial decreases in the amounts of time spent sleeping, inactive, feeding, moving within trees and walking between trees. Furthermore, individuals with advanced tooth wear spent longer feeding per bout, spaced the feeding bouts out more regularly throughout a 24-h period and deviated further from true nocturnality than did individuals with less worn teeth. Hence, it is concluded that tooth wear does have the potential to impose severe limitations on the activity patterns, time budgeting and sociability of free-ranging koalas. It is therefore considered to be a very important ecological process that has the capacity to influence the structure and dynamics of wild animal populations. It is, however, acknowledged that much of this discussion is based on the data from just six individuals. However, the data are consistent with the findings of other studies and do offer one potential explanation for some of the behavioural differences reported between individual koalas.

Acknowledgments

We thank Natalie Lloyd immensely for assisting in the capture of koalas throughout this study, providing moral support, and commenting on manuscript drafts. M. Logan also acknowledges the generous support of Deborah and Bill Thompson of A'Beckett Park (Raymond Island) for providing battery charging facilities. We also thank the two referees, whose comments greatly improved the manuscript. This study was carried out with the permission of the Department of Natural Resources and Environment (Permit No. 10000198) and the Monash University Animal Ethics Committee, and was supported by funds made available by the Collier Charitable Fund and Monash University.

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