The association of tooth wear with sociality of free-ranging male koalas
(Phascolarctos cinereus Goldfuss)

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Abstract

The sociality (as measured by the degree of bellowing and amount of tree use) of five adult male koalas and one sub-adult male koala (Phascolarctos cinereus), with varying degrees of tooth wear, were investigated using acoustically sensitive radio-telemetry. Initial increases in tooth wear that coincide with an increase in age to maturity were associated with an increase in reproductive effort. Advanced tooth wear was found to be associated with a decrease in reproductive effort. This trend in reproductive effort is consistent with life-history predictions, and suggests that tooth wear has the potential to impose limitations on the reproductive longevity and fecundity of free-ranging male koalas.

Introduction

Logan and Sanson (2002a) described the consequences of increasing tooth wear on the feeding behaviour of free-ranging male koalas. Adult male koalas were found to compensate for increased tooth wear by increasing the amount of time and effort they spent feeding. Increased tooth wear was found to be associated with a daily increase in leaf consumption, chews per leaf, chew rate, time spent feeding and total number of chews. Furthermore, this increased feeding investment was found to have an impact on the duration and timing of other, non-feeding activities (Logan and Sanson 2002b). In fact, Logan and Sanson (2002b) found that male koalas with high degrees of tooth wear spent substantially less time moving within and between trees, and had home-range sizes an order of magnitude smaller than those of other males. Logan and Sanson (2002b), therefore suggested that advanced tooth wear may also result in a reduction in sociality. This, in turn, may indicate a decrease in reproductive effort and reproductive output.

Male koalas form dominance hierarchies that are believed to be based on aggressive encounters in which dominant males attempt to prevent other males from mating (Mitchell 1990). However, koalas are inactive, solitary, sedentary and nocturnal in habit. Consequently, individuals engage in relatively few direct interactions (Mitchell 1990) and the effectiveness of visual communication is greatly restricted. Instead, range boundaries and dominance hierarchies are thought to be maintained and advertised via scent marking and bellowing (Mitchell 1990). Scent is deposited onto the branches and trunks of trees by male koalas via a sternal gland (Smith 1980b). Male koalas are more likely to scent mark trees that have previously been occupied by another male (Mitchell 1990), or that are less familiar (Smith 1980b). This suggests that a male koala advertises his presence and/or dominance by depositing scent on many of the trees within his range, not just the ones he uses for feeding. Hence, dominant males may be expected to "use" more trees than subordinate males. If so, then the degree of non-feeding tree use is likely to be an indication of social position and a measure of the individuals’ reproductive effort.
The bellowing behaviour of male koalas has also been well described (Smith 1980a; Mitchell 1990), and is believed to have a reproductive role whereby the distances between neighbouring males can be maintained with minimal aggressive encounters. Therefore, the amount of time an individual spends bellowing is also likely to be a good indication of the individual’s position within the social hierarchy and a measure of reproductive effort.

The aim of the present study was to investigate the association of tooth wear with tree use, bellowing behaviour and, thus, the sociality and reproductive effort of free-ranging male koalas.

Materials and Methods

This study was carried out in conjunction with investigations into the effects of tooth wear on the feeding behaviour (Logan and Sanson 2002a) and activity patterns (Logan and Sanson 2002b) of free-ranging koalas. Consequently, more complete descriptions of the study site, catching procedures and field equipment is given by Logan and Sanson (2002a). One sub-adult male and five adult male koalas of varying degrees of tooth wear, were captured from a wild population on Raymond Island (off Paynesville, 300 km east of Melbourne, Victoria), and fitted with newly developed, acoustically sensitive radio-transmitters (Sirtrack Ltd). Each transmitter was mounted on a standard wildlife collar and was capable of detecting and transmitting all audible sounds made by an animal.

Tooth wear was established on the basis of the descriptions of tooth wear classes by Martin (1981) and confirmed by the descriptions of Lanyon and Sanson (1986) and Gordon (1991). When premolar wear features were between the classes described by Martin (1981), fractional scores depicting the degrees 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 continuous scale potentially ranging from 0.0 (unworn) to 7.0 (completely worn or absent). Following a period of at least 72 h (after release) in which the animals were able to recover and transmitted sounds could be calibrated against observed activities, the sounds made by each individual were recorded onto VCR tapes continuously over 24 h during two non-consecutive 24-h periods (commencing at 16:00 hours).

VCR tapes were later played back in synchrony with event-recording software (written by M. Logan). All audibly discernible activities were thereby digitally ‘flagged’ together with the exact time and date at which they occurred. The duration of events was then expressed as the average amount of time (min.) spent per 24 h, and the average number of bellowing bouts per individual per 24 h was calculated. The number of trees used per individual per 24 h was calculated as one plus the number of times the individual changed trees (as indicated by the number of climbing–walking–climbing sound sequences detected). During the time of recording, sound signals were continuously monitored by a remote observer (from a distance of 100–200 m). Whenever sound signals indicated a potential change in tree (e.g. climbing and/or walking sounds) the individual was located to confirm tree use and to determine whether the change in tree represented the use of a new tree or a tree that the individual had previously visited throughout the recording session. Tree use was categorised as either feeding or non-feeding on the basis of the presence or absence of recorded feeding bouts whilst the individual was in the particular tree. Therefore, the average number of trees used for feeding purposes per individual per 24 h was calculated as the number of times one or more feeding bouts were detected between two consecutive tree-changing events.

Results

Individuals in the Tooth Wear Range 2–3 were found to spend substantially more time bellowing than individuals with either low (<2) or high (>4) degrees of tooth wear (Fig. 1). Furthermore these individuals were found to use more trees per 24 h than adult individuals with low or high degrees of tooth wear (Fig. 2). The sub-adult was also found to use a relatively large number of trees per 24 h. The increase in tree use was not found to correspond to an increase in the average number of trees used for feeding activities, which were similar for each individual (Fig. 2). Rather, the increase in tree use was attributed to an increase in use for non-feeding-related activities.
Discussion
Logan and Sanson (2002a) demonstrated considerable differences in the amount of leaf material consumed per 24 h by different individual koalas, and that such differences were strongly associated with the degree of tooth wear. Despite these differences, however, the present study shows that all individuals were found to use a similar number of trees per day for feeding purposes (Fig. 2) and that there were no obvious relationships between tooth wear and the number of trees used for feeding. However, adult individuals with tooth wear in the range 2–3 were found to have higher non-feeding tree use than other individuals, and these individuals were also found to spend more time bellowing than did other individuals (Fig. 1). This observation suggests that these two individuals were investing more in active dominance (and thus greater reproductive effort) than other individuals with either low (<2) or high (>4) degrees of tooth wear.

Logan and Sanson (2002b) found that while the home ranges of these two medium-tooth-wear individuals were substantially larger than the ranges of the two individuals with high tooth wear, they were not larger than those of the adult and sub-adult with low tooth wear. Therefore, it is unlikely that the increased tree use is purely a
consequence of increased range size. Instead, these two individuals use a greater proportion of the trees within their ranges, which may enable them to advertise and maintain dominance.

The adult with very low tooth wear used fewer trees for non-feeding purposes and spent considerably less time bellowing per 24 h than did the individuals with low to medium tooth wear. This suggests that the tree use of this individual is mainly driven by the need to acquire fresh leaves rather than to maintain social standing or home range. Its range and position in the social hierarchy are likely to have been defined by the boundaries and sociality of neighbouring individuals.

The two high-tooth-wear individuals did not use extra trees in addition to those used for the purpose of feeding (see Fig. 2). This further supports Logan and Sanson’s (2002b) suggestion that these individuals changed trees solely for the purpose of obtaining fresh leaves, rather than to maintain a hierarchical position. Although these individuals consumed considerably more leaf material than did the other individuals (see Logan and Sanson 2002a), they did not use any more trees while feeding. Logan and Sanson (2002b) suggested that the compensation employed by these two koalas in an effort to offset the effects of reduced masticatory effectiveness may ultimately reduce the amount of time and energy the individuals have available to devote to other activities. In addition, these two individuals were found to spend a very small amount of time bellowing (similar to the young subordinate individuals). Again, this suggests a reduction in social maintenance and thus reproductive effort.

Consistent with Smith’s (1980a) finding that sub-adults rarely bellow, the sub-adult individual was not found to engage in any bouts of bellowing. However, he was found to use a large number of trees for non-feeding purposes. During the time of the investigation, this individual had a much larger home range than did the other individuals (Logan and Sanson 2002b) and was thought to be dispersing. As a result, antagonistic encounters were frequent, and on many occasions it exited a newly entered tree after sniffing the trunk and branches or after it was challenged by another male. Hence, the high amount of tree-use for non-feeding purposes by the sub-adult was likely to be the result of dispersal behaviour, rather than as a show of aggression or advertisement towards other individuals.

The relationship between bellowing and tooth wear illustrated herein, has also been described (without discussion) in terms of koala age by Smith (1980a). Similarly, trends in reproductive effort have been associated with age in bison (Maher and Byers 1987). Maher and Byers (1987) investigated the age-related changes in reproductive effort of male bison (*Bison bison*) and found that reproductive effort initially increased with age, before reaching a plateau during the prime years, and finally decreased again in association with old age. They argued that this was brought about by a U-shaped relationship between age and the ratio of costs to benefits associated with reproductive participation and was consistent with life-history theory. In young individuals, the benefits of reproductive effort relative to the high costs of reproduction (both energetic and risks) are low and improve with age. As a result, young individuals show an increase in reproductive effort with age. As males progress through puberty, maturity and dominance, this cost–benefit ratio declines and finally flattens, due to increases in fighting ability. Eventually, the costs of reproductive effort relative to the benefits increase again as the individual moves into and through old age, thus resulting in a decline in reproductive effort. Often, old age is also associated with other physiological constraints that could further preclude reproductive behaviour.
Male koalas, like male bison, do not exhibit parental care, and therefore competition for copulations is the major component of their reproductive effort. Consequently, koalas might also be expected to exhibit a U-shaped relationship between age and the cost–benefit ratio of reproductive effort. It is perhaps not surprising, therefore, that koalas appear to demonstrate a similar trend in reproductive effort (as indicated by the relationships between degree of bellowing and non-feeding tree use and degree of tooth wear) to that of the bison.

Tooth wear is a function of the number of times the teeth have occluded and the abrasiveness of the masticated food material, and is therefore only indirectly related to age. Nevertheless, within a given population, the teeth of older individuals are likely to have occluded more often (and thus have higher degrees of wear) than those of younger individuals.

Mature koalas with very low degrees of tooth wear are likely to be young individuals. The benefits of reproductive effort relative to the costs for such individuals are likely to be relatively low, and as a result, reproductive effort is low. Individuals with low-to-medium degrees of tooth wear are likely to be more socially skilful than the young inexperienced individuals. For such individuals, the reproductive cost–benefit ratio becomes more favourable, resulting in an increase in reproductive effort. Individuals with high tooth wear, whilst not necessarily representing an older demographic, are likely to have less energy and time available to expend on reproductive effort. Consequently, the costs of reproductive effort are large relative to the benefits, resulting in a decrease in reproductive effort. In koalas, tooth wear (and the effects thereof) is the major change that occurs with age (P. Mitchell, personal communication). Therefore, a decrease in reproductive effort is likely to be a result of a decrease in energy availability.

Interestingly, Maher and Byers (1987) indicated that the degree of reproductive effort amongst individuals in the oldest age group was highly variable. Tooth wear is a process that can affect the behaviour and activity patterns of herbivores (Perez-Barbera 1989; Logan and Sanson 2002a, 2002b), and its severity increases with increasing age. However, as mentioned, age is not the only factor affecting tooth wear and, thus, the degree of variability of tooth wear usually increases with increasing age (e.g. Gordon 1991). Hence, the high variability in reproductive effort between old male bison may, in part, be due to high variability in the degree to which their teeth are worn.

Although it is acknowledged that the above conclusions are based on a small number of individuals, the enormous investment of time required to obtain this quantity and quality of data per individual per 24 h currently prohibits greater sample sizes. The results do suggest that tooth wear has the potential to impose limitations on the sociality and reproductive output of free-ranging male koalas. The implications are that individuals from populations that experience a greater rate of tooth wear are likely to have shorter reproductive lifespans. Ultimately, this could equate to lower fecundity, a situation observed by Pahl (1987) in another aboreal folivore, the ringtail possum (*Pseudochirus peregrinus*).

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