A review of feeding and diet selection in koalas (*Phascolarctos cinereus*)

Benjamin D. Moore and William J. Foley

Division of Botany and Zoology, Australian National University,
Canberra, ACT 0200, Australia.

Abstract

Food quality and availability are believed to be primary determinants of habitat quality for koalas (*Phascolarctos cinereus*), so we need to know 'what makes good food for koalas?' An answer to this question must define the dietary niche of koalas, describe how much koalas eat and also consider variation in food choice by koalas at several scales. Ultimately, all these issues must be related to variation in foliar chemistry. Recent studies have shown that there is a closer relationship between leaf composition and the food preferences of koalas than had previously been appreciated but we emphasise the importance of evaluating diet selection within a theoretical framework and at appropriate temporal and spatial scales. Finally, we discuss the steps needed to incorporate an understanding of the nutritional challenges faced by koalas into a broader understanding of the species' ecology to assist in its conservation.

Introduction

Habitat quality for an animal species can be influenced by a number of factors. Animals have requirements for food and shelter and are adversely affected by competition and predation. The koala (*Phascolarctos cinereus*), however, has few natural predators, does not have specialised requirements for shelter (Martin and Handasyde 1999) and does not appear to be limited by interspecific competition (Norton and Neave 1990). Accordingly, it has been proposed that food availability is the primary determinant of koala habitat quality (Norton and Neave 1990; Melzer and Houston 1997). Any attempt to understand what influences the quality of habitat for this species and what factors influence its foraging decisions should begin by asking the question 'what makes good food for koalas?'

This question has been the subject of much investigation and speculation but scant regard has been paid to the question of how koalas' preferences develop. Some studies have focussed on preferences for eucalypt species, whereas others have attempted to determine the nutritional constraints under which koalas forage and how palatable foliage differs chemically from unpalatable foliage. The question needs to be answered in the context of a framework of diet selection, which should identify the reasons why an animal selects the diet that it does and be able to address the way in which the animal deals with the foraging challenges facing it. It should also be able to explain why individual animals can have different dietary preferences. Initially, we can approach the question by asking two very basic questions about the koala's dietary habits: what is the koala's niche? and how much do koalas eat?

What is the koala's niche?

The koala has long been recognised as a specialised folivore of *Eucalyptus* (Martin and Handasyde 1999), but the extent to which koalas rely on eucalypts and the number of different eucalypt species that individuals and populations of koalas regularly use can vary considerably. This is relevant not only to our understanding of how individuals and populations of koalas forage, but also to our understanding of what koalas are able to eat and of the variety of nutritional challenges that they are able to meet.

Across their range, koalas have been observed eating or sitting in 120 different eucalypt species (Phillips 1990). During the 1985–86 National Koala Survey, reported by Phillips (1990), koalas were observed sitting in, or eating from, 69 different eucalypts and almost 30 non-eucalypts. From a list of eucalypt species reported to be suffering dieback, Pahl *et al.* (1990) identified 55 species that were recognised as koala food species, of which 18 were considered primary food species. The taxonomic diversity of food species available to koalas, then, appears to be considerable. Numerous studies have observed non-eucalypts to constitute at least minor proportions of koala diets. Hasegawa (1995) found that *Melaleuca quinquenervia* comprised up to 7% of koalas' diets at Point Halloran, while U Nyo Tun (1993) found that *Lophostemon confertus* was amongst the four most preferred food species in his study and another study at Pine Creek State Forest found *Allocasuarina torulosa* in 70% of koala scats (State Forests of New South Wales 1997). This latter study also found individual koalas to be feeding from an average of 10 and as many as 15 different tree species, from the 10 eucalypts and 9 non-eucalypts utilised by the population. Nonetheless, most studies of koala feeding habits have found that they predominantly feed on one or a few eucalypt species at any site.

That koalas are 'fussy' eaters has long been an article of folklore. As early as 1803 it was reported that 'its food consists solely of gum leaves, in the choice of which it is excessively nice' (Troughton 1935). More recently, it has been argued, on the basis of the large number of species from which koalas are now known to feed, that they are perhaps more generalist feeders than has been previously recognised (Phillips 1990). That koalas should eat the foliage of so many different species is not surprising – they do not select food on the basis of its taxonomy. Rather, a koala could be expected to eat any foliage with the appropriate morphology and chemistry to allow it to be recognised as palatable food. Just how fussy a koala's diet selection is, then, should be considered in terms of those chemical properties relevant to its nutrition. The chemical breadth of the koala's dietary niche might actually be quite large when compared with that of other folivores of *Eucalyptus* (e.g. Lawler *et al.* 1998*a*).

How much do koalas eat?

The question 'how much do koalas eat?' is not a trivial one, as measures of the absolute intake of foliage are essential if we are to quantify the role of leaf composition in determining the palatability and nutritive value of foliage. Many studies have considered koala dietary preferences by visually estimating intake by koalas in 'choice' experiments where intake of leaf from several different species is compared (e.g. Congreve and Betts 1978; Pahl and Hume 1990; Hume *et al.* 1996), or by recording the amount of time spent by koalas in particular trees (e.g. Eberhard 1972; Hindell *et al.* 1985; Hindell and Lee 1987; White and Kunst 1990), but direct gravimetric measures of intake from different trees are less common.

Table 1 lists eight studies that have estimated food intake by koalas. Three of these studies used the turnover rates of isotopes of water to estimate food intake by free-ranging koalas. These measures are important as they indicate the 'normal' amount eaten by free-ranging koalas and this is an important benchmark with which to compare intakes from particular trees. Four of these studies measured intake, primarily of *Eucalyptus punctata*, by captive koalas in metabolism cages during the course of broader studies of koala digestion and metabolism and one study measured intake of leaf from individual trees of *E. viminalis* and *E. ovata* by captive koalas in pens. Cork *et al.* (1983) concluded that intake by koalas on a diet of *E. punctata* foliage was low relative to that of other animals and attributed this to the koala's low basal metabolic rate.

Apart from Krockenberger's (1993) results, which are notably higher, most studies of intake by free-ranging koalas have produced similar results to those of captive koalas. It is also notable that all studies that measured intake separately in summer and winter observed higher intakes in the latter season, a fact that could be expected to influence koala diet selection (discussed below).

Only one published study has measured the intakes of foliage by koalas from a range of individual trees within a species (Lawler *et al.* 1998*a*). Whereas experiments that offer animals a choice between two or more different food types can tell us only if one of these is preferred relative to the others, no-choice experiments indicate how much of a food an animal is capable of ingesting. If it refuses to eat more than a certain amount, it is not merely because it prefers another type of available food, but because it is not prepared to eat any more of the food available. Lawler *et al.* (1998*a*) found considerable intraspecific variation in dry matter intake among five *E. ovata* and five *E. viminalis* (Table 1). This variation in palatability between individual trees represents an important level of diet selection that should not be ignored.

Foraging challenges faced by koalas

Like all herbivores, koalas face certain challenges when foraging (Provenza and Balph 1990), including variation in nutrients between foliage from different trees and between different leaf age classes. Plant defences can also vary both between and within species (Cork and Foley 1991, 1997; Lawler *et al.* 1998*a*). Plants can develop various morphological defences and in the case of koalas, the use of trees for purposes other than feeding and their preference for larger trees (Hindell and Lee 1987) would suggest that tree structure and/or size has some bearing on tree selection. The sclerophyllic nature of eucalypts also represents a potential morphological defence. Koalas are faced with both temporal and spatial variation in the quality and quantity of foliage and all of these foraging challenges are further compounded for dispersing or translocated koalas when they are forced to forage in unfamiliar environments.

Seasonal variation

Early commentators reported that the koala's preferences for certain eucalypt species, particularly *E. viminalis*, change with the seasons (Fleay 1937; Pratt 1937). While Williams (1971) and Fleay (1937) both reported that *E. viminalis* was the species preferred by koalas at Melbourne Zoo for all seasons of the year other than winter, when it was rejected, George (1977) observed that captive koalas at Healesville Sanctuary ate *E. viminalis* year-round.

Table 1. Published estimates of food intake by koalas
Estimates were determined by a number of techniques over 24 h

Method of estimation	Location	Tree species	DM intake ($g \cdot kg^{-0.75} \cdot day^{-1}$)	Study
$^3H_2^{18}O$	Walkerville, Vic.	Mixed	43	Nagy and Martin (1985)
^3H_2O	Nowendoc, NSW	Mixed	51 (summer) 57 (winter, non-lactating) 71 (winter, lactating)	Krockenberger (1993)
^3H_2O	Springsure, Qld	Mixed	34 (summer) 42 (winter)	Ellis *et al.* (1995)
Gravimetric	Captivity	*E. punctata*	31	Eberhard *et al.* (1975)
Gravimetric	Captivity	*E. punctata*	41 (summer) 46 (winter)	Harrop and Degabriele (1976)
Gravimetric	Captivity	*E. punctata*	41	Cork *et al.* (1983)
Acid lignin as internal marker	Captivity	Mixed	25–31[A]	Ullrey *et al.* (1981*b*)
Gravimetric	Captivity	*E. ovata* *E. viminalis*	22–36[B] 14–46[B]	Lawler *et al.* (1998*a*)

[A]Because acid lignin of eucalypts is invariably digested (Cork *et al.* 1983) this method could be expected to overestimate intake.
[B]Range of values indicates intakes recorded from several individual trees over 13 h overnight.

Eberhard (1972) found that free-ranging koalas on Kangaroo Island favoured *E. viminalis* in winter, whereas Hindell and Lee (1987) found that koalas in the Brisbane Ranges preferred *E. viminalis* in autumn, winter and spring, but shifted their preference to *E. ovata* in summer. Williams (1971) and George (1977) also observed that captive koalas' preference for *E. radiata* increased in summer, and the latter study reported the same for *E. obliqua* in late winter and spring. In another study of free-ranging koalas, Martin (1985) described a declining preference for *E. ovata* at Walkerville in spring and summer and an increased reliance on *E. obliqua* and *E. radiata*. Congreve and Betts (1978) reported that the preference of captive koalas in Western Australia for *E. globulus* increased between May and February. Krockenberger (1993) found that koalas at Nowendoc selected foliage within species on different nutritional criteria in summer and winter.

It is possible that shifts towards particular species at certain times might be explained by flushes of new growth on these species, which occur seasonally throughout the range of the koala (Specht and Brouwer 1975). In particular, reported seasonal shifts to *E. radiata*, *E. obliqua* and *E. ovata* seem to coincide with such flushes. However, it may not be the case that the young leaf of all eucalypt species or individuals is preferred to the mature leaf (discussed below). In several of the reported cases involving *E. viminalis*, a clear rejection of foliage from trees that were acceptable for most of the year was evident. Pratt (1937) believed that this was due to an increased concentration of toxic compounds, which he believed to be cyanogenic glycosides. These secondary metabolites had been previously identified in some *E. viminalis* by Finnemore *et al.* (1935). Congreve and Betts (1978) also found that *E. viminalis* from a plantation in Western Australia, which was consumed by koalas for most of the year, occasionally tested positive to cyanide during the wetter months of July and August, at which time the koalas' response to it was more 'variable'. More recent and widespread surveys of *E. viminalis*, however, indicate that cyanogenic glycosides are not common in this species (Martin and Handasyde 1999). It is also conceivable that seasonal changes in feeding preferences are associated not with phenology, but with seasonal changes in the koala's physiology and nutritional demands associated with altered needs for thermoregulation.

Seasonal changes in koalas' preferences might be explained in some instances by a changing need for, and availability of, water. In semi-arid northern Queensland (Munks *et al.* 1996) and in drought conditions in south-western Queensland (Gordon *et al.* 1988) koalas were shown to use trees with higher than average leaf moisture. Several studies have also proposed threshold requirements for leaf moisture (Pahl and Hume 1990; Hume and Esson 1993), including Melzer (1995*a*), who found a higher threshold in November than in September.

Several studies (Table 1) have found that koalas eat more in winter than in summer, presumably to accommodate the higher field metabolic rates (Ellis *et al.* 1995). The altered nutritional demands implied by these studies may be met by adjusting diet selection strategies as well as by varying intake. Krockenberger (1993) found that free-ranging lactating female koalas not only ate more leaf than non-lactating koalas, but they also selected leaf in some months that contained less total phenolics and a higher ratio of nitrogen to total phenolics. At the population level this may be reflected in changes in diet selection correlated with the breeding season. To understand the scope for diet selection by free-ranging koalas, seasonal changes in the availability and quality of food need to be considered in the context of a good understanding of the nutritional basis of diet selection and how this basis might vary seasonally with changing nutritional demands.

Regional variation

Preferences for particular eucalypt species may also differ from region to region. Unfortunately, it is difficult to separate the effect of regional differences in species' palatability from differences in preference due to the presence of different suites of alternative food species. One example from captive studies concerns *E. microcorys*, which is recognised as a key species for koalas on the mid and far north coast of New South Wales and in coastal south-east Queensland (Bergin 1978;

Clarke 1980; U Nyo Tun 1993; Pahl 1996). Pahl and Hume (1990) offered four trees of *E. microcorys* to a group of captive koalas at Armidale and found it to be among the least preferred of 18 eucalypt species from the Northern Tablelands of New South Wales. The koalas came from French Island in Victoria and had previously encountered only one of the eucalypt species in this study, yet rapidly formed strong preferences for several new species. Therefore, novelty alone would not seem to explain the koalas' rejection of *E. microcorys*.

Although many studies in Victoria have found *E. viminalis* to be highly preferred (Lithgow 1980; Hindell 1984; Menkhorst 1995), Hindell *et al.* (1985) reported that certain koalas on Phillip Island were consistently found in *E. globulus*, despite the nearby presence of *E. viminalis*. When these koalas were taken into captivity, they still preferred *E. globulus* to *E. viminalis* (the source of this leaf was not stated). In a more recent study at an adjacent site containing *E. globulus*, *E. ovata* and *E. viminalis*, Bednarik (1996) found that all individual koalas that showed significant preferences for a tree species showed that preference for *E. globulus*.

Martin (1985) found that *E. radiata* showed no evidence of being browsed and was rarely occupied by koalas at Walkerville, Victoria, even while the resident koalas were defoliating their preferred tree species, causing them to disperse or suffer loss of condition and fecundity and increased mortality. However, this species was used by koalas in proportion to its abundance in Krockenberger's (1993) study in north-eastern New South Wales, accounting for 14% of observed tree use. It also accounted for 6% of sightings in Victoria during the 1985–87 National Koala Survey (Phillips 1990).

These regional differences may be due to varying nutrient concentrations and/or to qualitative or quantitative variation in the defensive compounds present in some eucalypt species throughout their geographic range. It is also possible that koalas in different parts of their range may have quite different responses to local environmental conditions and to local eucalypts. Some morphological differences between southern and northern koalas are obvious (Martin and Handasyde 1999), but there may also be differences in their nutritional needs and in their capacity to tolerate plant secondary metabolites. Studies in common ringtail possums (*Pseudocheirus peregrinus*) by Lawler *et al.* (1998b) showed that there were differences between northern and southern populations in their tolerance of purified jensenone (a secondary metabolite of *Eucalyptus* with a known antifeedant effect) incorporated into an artificial diet. Observed differences in the preferences of individual koalas (Hindell *et al.* 1985; Hindell and Lee 1988) for particular tree species suggests that preferences could vary in a similar fashion between regions. Although we do not understand the aspects of koala physiology that might vary in such a way to explain these regional differences, some aspects of leaf chemistry that influence leaf palatability are understood (discussed below) and currently offer the most promising avenue for investigating their cause.

Intraspecific variation

Numerous studies have shown that koalas often prefer certain individual trees within a species (Fleay 1937; Eberhard 1978; Robbins and Russell 1978; Hindell *et al.* 1985; Hindell and Lee 1987). These preferences may be partly explained by structural attributes of the trees, as a number of studies have detected preferences for large trees (Hindell and Lee 1987; White 1994; Hasegawa 1995; Melzer 1995a; Lunney *et al.* 1996). As koalas establish home ranges comprising certain individual 'home range trees' (Mitchell 1990a) the preference for individual trees might also be explained in large part by a reluctance to use unfamiliar trees. However, evidence that captive koalas also show preferences for foliage from individual trees within many species (Williams 1971; Pahl and Hume 1990; Lawler *et al.* 1998a, see Table 1) suggests that leaf composition also plays a role. Lawler *et al.* (2000) also found individual variation in the intake of *E. polyanthemos* and *E. sideroxylon* by captive common ringtail possums, suggesting that intraspecific variation is not an uncommon phenomenon.

Variation between individual trees within a species has been little considered in studies of foraging by koalas. Recent studies (reviewed below) that have considered intraspecific

variability have been able to demonstrate a strong chemical basis for food selection by marsupial folivores; between-tree variation in palatability therefore represents a major foraging challenge for koalas.

The role of leaf age in diet selection

Koalas do not only assess the quality of foliage at the scale of the individual tree. When feeding, koalas carefully assess individual branchlets before deciding whether to accept or reject them (Smith 1979*a*). One cause of varying palatability within trees is differences between young and old leaf: many authors have noted that koalas prefer young foliage when it is available (Fleay 1937; George 1977; Congreve and Betts 1978; Degabriele 1981; Ullrey *et al.* 1981*a*; Cork 1984; Hindell 1984; Pahl and Hume 1990) and hypotheses have been extended concerning the requirements of koalas for forests with mixtures of species in which at least one tree species will be producing new growth at most times of the year (Cork *et al.* 1990). The greater glider (*Petauroides volans*) and the common ringtail possum also generally prefer young foliage of *Eucalyptus* over older leaves (Pahl 1984, 1987; Henry 1985; Hume *et al.* 1996) although Thomson and Owen (1964) reported that the latter species did not eat the young foliage of eucalypts in their study. However, only one study has compared intake of young and old leaf from known individual trees, a necessary step if the effects of leaf age are to be separated from intraspecific variation. Pahl and Hume (1990) visually estimated the preferences shown by captive koalas for young and old foliage from individual trees of 18 species but only reported average preference indices obtained from four trees for each species. They concluded that, for each of the 14 species eaten by koalas, young leaf was preferred but the strength of this preference was not quantified.

Despite the number of reports listed above, a preference for young leaves may not be universal for all trees. Pratt (1937) observed that koalas rejected the young leaves of juvenile trees, especially of *E. viminalis*, and Hindell (1984) reported that although koalas preferentially consume young foliage at the start of a feeding bout they then go on to consume large amounts of older leaf. The only study of the long-term contribution of young and old leaf to koala diet is that of U Nyo Tun (1993). By analysing faecal leaf cuticle fragments, he found that young foliage accounted for 5–35% of the diet of four rehabilitated koalas, but mature foliage accounted for the greater part: 50–90% over a 12-month period. An important point made by Hindell *et al.* (1985) is that while captive koalas are often presented with bunched foliage bearing large proportions of young leaf, the equivalent leaf may not be so readily available to free-ranging koalas when it is dispersed throughout the canopy of a tree.

There is no clear reason why koalas should select younger rather than older leaves of *Eucalyptus*. Although younger leaves generally contain more nitrogen and water and less fibre than mature leaves, they also have higher concentrations of total phenolics (Cork and Pahl 1984; Hume and Esson 1993; Hume *et al.* 1996; Krockenberger *et al.* 1998). The contrast in oil yield between young and mature leaves varies in both the direction and extent of the differences, both between species and between individual trees within a population (Boland *et al.* 1991). The relative concentrations of a specific group of phenolic compounds, the formyl phloroglucinol compounds, or FPCs (discussed below) in young and old leaf is unknown. So although young leaves may contain greater concentrations of macronutrients than older leaves, the young leaf of certain species or individual trees, particularly those that are already highly defended, may contain toxins at concentrations too high for koalas to tolerate, while the leaves of other trees may be less defended.

An appreciation of the context in which younger leaf is preferred by koalas is important if we are to understand the quality and quantity of foliage available to koalas in their natural environment. This will be achieved only when quantitative measures are made of the relative intake of young and old foliage from known trees and related to appropriate measures of leaf composition.

Using a formal framework to understand diet selection

Five models have emerged that attempt to provide a framework to diet selection in herbivores (Provenza and Balph 1990). We will outline each of these models, review their previous application to diet selection by koalas and discuss their potential to provide a framework that will allow interpretation of existing data on diet selection by koalas and contribute to the collection of more appropriate data in the future.

Model 1: Euphagia

Euphagia describes an animal's innate ability to taste and smell specific nutrients and toxins in food. Although it has often been assumed (e.g. Betts 1978; Smith 1979*a*) that koalas select their diet on the basis of olfactory cues, the existence of an innate ability to discriminate between positive and negative cues is not recognised. The main weakness of this explanatory model is that the only established innate hungers are for sodium and calcium (Krieckhaus and Wolf 1968; Coldwell and Tordoff 1993, 1996), and although euphagia could conceivably explain the observed ingestion of soil and gravel by koalas (Bolliger 1962; Smith 1979*a*) it fails as a general explanation of diet selection. If water is considered to be a nutrient, however, an innate thirst drive (Zabik *et al.* 1993) could explain the selection of leaves above a moisture threshold when free water is not available.

Model 2: Hedyphagia

This explanation proposes that animals obtain a nutritious diet by selecting only vegetation that is 'pleasing' to the senses, based on the assumption that natural selection has caused nutritious compounds to taste good and toxic compounds to taste bad. The main weakness of this theory is that it offers no role for the post-ingestive consequences of food, although there is significant evidence that animals discriminate between foods on the basis of previous negative or positive experiences with particular flavours (Launchbaugh and Provenza 1993). It has been shown that post-ingestive consequences are associated with a group of secondary metabolites of *Eucalyptus* known as the formylated phloroglucinol derivatives or FPCs (Lawler *et al.* 1998*b*) and that these can play an important role in diet selection by common ringtail possums and common brushtail possums (*Trichosurus vulpecula*) (Lawler *et al.* 1999, discussed below).

Model 3: Body morphology and size

Another group of explanations of diet selection is based around the physiological and allometric constraints imposed by an animal's morphology and size, and it is these types of theories that have been most widely called upon to explain the koala's dietary niche. General allometric principles suggest that an animal the size of the koala should face severe difficulties surviving on a diet as high in fibre and low in nitrogen as mature *Eucalyptus* foliage (Cork and Sanson 1990; Cork and Foley 1991). It might be expected then that natural selection should favour larger size for the koala, yet the scope for this is limited by the animal's need for mobility in the treetops. As a result, a range of metabolic and physiological adaptations have evolved to allow the koala (and other smaller marsupial folivores such as the greater glider and ringtail possum) to cope with a diet of *Eucalyptus*, and the variation in body size between koalas in Queensland (females 5.1 kg, males 6.5 kg) and Victoria (females 8.5 kg, males 12.0 kg) (Strahan 1995) suggests that these adaptations provide considerable evolutionary plasticity within this body-size constraint.

The koala has numerous adaptations that allow it to cope with its poor-quality diet (Cork and Sanson 1990), including extremely low energy requirements, a specialised dentition, and a mechanism allowing the separation of small and large leaf particles in the digesta, which facilitates the rapid passage of large fibrous particles and the prolonged retention of smaller particles in the highly developed caecum and proximal colon. These adaptations are also developed to varying extents in the greater glider, and the ringtail and brushtail possums (Cork and Foley 1997).

The importance of the koala's size, morphology and physiology has been investigated by many studies (Cork and Sanson 1990) that have attempted to provide explanations for how koalas cope with the challenges presented by their diet, and how the constraints under which they operate differ from those faced by other marsupial folivores of *Eucalyptus*. For example, ringtail possums are able to selectively remove mesophyll and palisade cells from between the highly fibrous midrib and lateral veins of leaves, but, because of their larger mouth, koalas must ingest entire leaves (Cork and Sanson 1990). This sort of explanation can often account for broad trends in diet selection between taxa, even to the level of species, but it tends to ignore the differences in diet selection between individual animals, such as instances where individual koalas show different preferences for particular trees. This sort of variation might be explained by individual variation in morphophysiology and neurology and by taking into account behavioural attributes of animals. This latter factor provides the focus for the next explanation of diet selection.

Model 4: Learning through foraging consequences

This explanation of diet selection assumes that animals are capable of learning to distinguish good food from bad on the basis of the positive and negative consequences associated with each, and has been reviewed extensively (Provenza 1995; Provenza *et al.* 1996, 1998). It proposes a detailed mechanism used by animals to address all the foraging challenges they face and explains differences between individual animals. Because of its detailed mechanistic nature, however, and the failure until recently to identify those components of eucalypt leaf that are most important in diet selection, it has not featured as a common explanation for diet selection by koalas. Clarke (1980) did propose that koalas' selectivity could be explained by their 'avoiding substances which previously they have associated with undesirable digestive experiences', but did not identify these substances.

A concept central to the learning model is the development of conditioned food aversions. These develop when animals learn to avoid a particular food because of an association between that food's sight, taste or odour and nauseous feedback (Provenza 1995; Provenza *et al.* 1996, 1998). This process does not depend on memory of the feedback event, but does require stimulation of the emetic (nausea) system. Many animals also appear capable of developing conditioned food preferences in a similar way. A conditioned food aversion has not been demonstrated in the koala, although it has been demonstrated (Lawler *et al.* 1998*b*) for two other folivores of *Eucalyptus*, the common ringtail possum and the common brushtail possum (discussed below). Conditioned food aversions associated with cyanide have also been reported in brushtail possums (O'Connor and Matthews 1995, 1997).

The learning model also accommodates a role for pre-ingestive experiences in the development of feeding preferences. Provenza and Balph (1990) list four types of pre-ingestive experience: *in utero* (which is probably less significant for marsupials than for eutherians); mother's milk; social; and individual trial and error. Another type that might affect koalas is pap feeding. Social pre-ingestive experiences include cases where young animals select foods that the mother eats. Such interactions are obvious in the koala as juveniles begin to eat leaf while riding on their mothers' backs. (Smith 1979*b*). Another example of a social interaction that potentially influences diet selection involves individual koalas using scent to identify particular trees upon which conspecifics feed. Koalas often pause to sniff the base or trunk of a tree (Eberhard 1972; Sharpe 1980; Russell 1985; Mitchell 1990*b*) and will scent-mark trees with urine (Mitchell 1990*b*) or, in the case of males, scent from a sternal gland (Sharpe 1980; Mitchell 1990*b*). This behaviour may make an environment more familiar for resident animals and, incidentally, allow koalas foraging in an unfamiliar environment to identify suitable feeding trees. Urine could potentially even provide olfactory information about the chemistry of a particular tree, as terpene metabolites are excreted in the urine (McLean and Foley 1997). Most significantly, though, by becoming familiar with their environment, koalas can overcome the challenges posed by temporal and spatial variation in the quality and quantity of foliage and avoid foraging in unfamiliar environments.

Because conditioned food aversions and preferences are dynamic, a koala can cope with unfamiliar foraging environments and with spatial and temporal variation in the quality of foliage by detecting changes in the concentrations of flavours in leaf from familiar food sources and by cautiously sampling novel foods (Clarke 1980). The learning model is also the only explanation that explicitly addresses individual variation in dietary preferences.

Model 5: Optimal foraging theory

The final explanation of diet selection presented by Provenza and Balph (1990) is optimal foraging theory (reviewed by Stephens and Krebs 1986). Optimal foraging theory assumes that animals forage in a way that will maximise nutritional gain per unit foraging cost and attempts to predict an optimal foraging strategy. However, the theory does not try to explain any underlying causal mechanisms. These models can take various forms, depending on the assumptions made concerning the currency being optimised (e.g. energy or nutrient gain, time minimisation), the types of decisions made by foragers (e.g. which dietary items to consume, how long to remain at a foraging location), and the constraints under which a foraging animal must operate (e.g. thresholds for the ingestion of particular nutrients or toxins, gut capacity). An optimal foraging model has not been applied to koalas although the questions of which nutrients koalas might attempt to maximise and of the nutritional constraints affecting them have been the subject of numerous studies reviewed here. Provenza and Balph (1990) concluded that this explanation is not well suited for determining whether or not diet choice is influenced by the nutritional composition of dietary items.

What influences diet selection?

All of the above models attempt to explain how koalas select good-quality food; however, most studies to date have been more concerned with determining the chemical characteristics that determine this. These have focussed both on the nutritive properties of *Eucalyptus* foliage and the role of putative toxins or anti-nutritional components. Most early discussions of the role of leaf chemistry in diet selection by koalas centred on the essential oils (e.g. Sutton 1934; Fleay 1937; Pratt 1937). Betts (1978) found a weak negative correlation between sesquiterpene content and koala preference for the leaf of *E. globulus*, but neither Southwell (1978) nor Eberhard (1978) found any relationship between feeding preferences and oil yield or composition. More recently, Hume and Esson (1993) reported that preferred foliage in their study had a higher proportion of volatile monoterpenes and a lower proportion of sequiterpenes, and met or exceeded a threshold concentration of total essential oils (2% of dry matter). Ullrey *et al.* (1981*a*) reported that preferred koala browse had higher concentrations of crude protein (and hence nitrogen), phosphorus and potassium and lower concentrations of fibre, gross energy, calcium, iron, selenium and a crude ether extract (which contained the essential oils and any other lipophilic components).

Leaf moisture thresholds of 55% and 65% have been proposed by Hume and Esson (1993) and Pahl and Hume (1990), respectively, whereas Melzer (1995*b*) identified two separate thresholds – 63% in November and 51% in September. Ellis *et al.* (1995) found that as water requirements of koalas in central Queensland increased in summer, the leaf moisture content of their food, and hence their water influx, increased correspondingly. Nonetheless, where free water is readily available, for example as dew, leaf moisture is probably of little consequence for diet selection.

Thresholds should be used cautiously to describe the properties of good koala food. As shown above, leaf moisture thresholds change with the demands of thermoregulation and cannot be applied to all eucalypt foliage under all circumstances. The same is true of thresholds of other nutrients – unless a broad range of tree species and individuals is considered, thresholds cannot be considered to be universal. For example, the essential oil threshold identified for the species used in Hume and Esson's (1993) study obviously does not hold for a great many other species

(e.g. *E. ovata*: Lawler *et al.* 1998*a*) that have very low total essential oil contents but are nonetheless favoured by koalas.

Leaf sugars are yet another group of leaf constituents that have been investigated for their possible role in diet choice of koalas. Osawa (1993) found that of those eucalypt species offered to captive koalas in Japan, those most preferred contained monosaccharides, but not di- and trisaccharides. However, he failed to find a significant correlation between sugar content and dietary preference.

Nitrogen

Largely on the basis of the findings of Ullrey *et al.* (1981*a*), Degabriele (1981; 1983) proposed that nitrogen was the major limiting influence on the abundance of the koala and that koalas select for low fibre content, which is usually correlated with high foliar nitrogen levels. Hume and Esson (1993) also found that the foliage preferred by koalas in their study had higher ratios of nitrogen to fibre and to condensed tannins, whereas Pahl and Hume (1990) reported a threshold of 1.8% for nitrogen, above which leaf was accepted by captive koalas. However, Cork (1986) found that koalas were capable of maintaining positive nitrogen balance on foliage containing as little as 1.1% total nitrogen, and estimated that the critical value was closer to 1.0%. As a result, it has been proposed that the concentration of nitrogen itself in most eucalypt foliage should not pose major problems (Cork and Sanson 1990; Cork and Catling 1996).

Regardless, published values suggest that low foliar nitrogen concentrations might exclude koalas from many areas. Mean values for 14 of 33 species sampled by Braithwaite *et al.* (1983) in the Eden woodchip concession area fell below Cork's 1.0% threshold (the lowest was 0.69%) and several studies with captive animals have reported low nitrogen values too (e.g. 0.94% and 0.82% in *E. polyanthemos* and *E. punctata*: Ullrey *et al.* 1981*a*; 0.92% in *E. punctata*: Harrop and Degabriele 1976; 0.83% in *E. caliginosa*: Pahl and Hume 1990). Hume *et al.* (1996) found that mean nitrogen values for *E. haemastoma* and *E. punctata* at Manly Dam were 0.74% and 1.00% in summer and 0.97% and 1.09% in winter – it would seem that many trees at a site like this would not provide suitable browse for koalas if the threshold values identified are accurate. In contrast, foliar nitrogen concentrations in areas used by free-ranging koalas are considerably greater than 1.0% (e.g. Nagy and Martin 1985; Krockenberger 1993; Bednarik 1996). It seems plausible, then, that a nitrogen threshold might have a valuable role to play in a hierarchical model of koala diet selection – if foliage is deficient in nitrogen, then it will be unable to sustain a herbivore regardless of the concentration of anti-nutrients or toxins present.

The stage at which nitrogen concentrations might affect koalas' assessment of the nutritional quality of leaf is not clear. There is no evidence that koalas can directly sense nitrogen concentrations before ingesting leaf, so euphagia can be rejected as an explanation. If nitrogen concentration is important to diet selection, koalas presumably (i) select leaf on another basis such as its secondary chemistry and then receive post-ingestive feedback about nitrogen, (ii) use a 'rule of thumb' such as 'always select young leaf from these species' to consistently select the highest nitrogen foliage available, or (iii) use another leaf property that is correlated with nitrogen concentration (such as fibre or a secondary compound) to indicate whether nitrogen levels are adequate.

In a broader, landscape-scale study, Braithwaite *et al.* (1983) found that threshold foliage concentrations of nitrogen, as well as phosphorus and potassium, could be used to identify eucalypt communities that can support viable populations of arboreal marsupials, including the koala (although great variation exists in population densities found in communities above this threshold). Although this study was successful at predicting landscape-scale trends, it does not necessarily follow that nitrogen concentrations determine diet selection at the scale of the leaf. The approach taken by this study was to calculate mean macronutrient concentrations from up to 22 (mean = 7) individual trees for each species and to multiply these by the proportion of tree basal area attributable to each species at each site. The sum of these values provided an estimate of mean macronutrient concentration for the site. Unfortunately, this approach does not consider

intraspecific variation in foliar constituents, which may occur within and between sites. Macronutrient estimates for each site represent what a folivorous marsupial would encounter if feeding randomly (Cork 1992), yet several studies (discussed above) have shown that koalas and other marsupial folivores of *Eucalyptus* are selective at several levels, including tree species, the individual tree and leaf age class. Even in situations where the estimate of foliar nitrogen for a community falls below certain threshold levels, certain species or trees in the community might meet or exceed that concentration and provide adequate foraging opportunities if koalas adopt an optimal foraging model allowing them to maximise nitrogen intake.

Cork (1992) and Cork and Catling (1996) proposed that a ratio of nitrogen to total phenolics should provide a better measure of leaf quality than nitrogen alone, as the quality of a foliage diet depends on the balance of the nutrients it provides and the costs associated with coping with its secondary metabolites. Using the dataset of Braithwaite *et al.* (1983), Cork (1992) found that this ratio could also identify those patches of forest used by most arboreal mammals, although it did not improve markedly on the results based on nitrogen alone. This result may also be explained by the failure of the sampling technique to consider intraspecific variation, as concentrations of certain phenolics show considerably greater variation both between and within species than do amounts of nutrients (discussed below).

The role of formylated phloroglucinol compounds (FPCs)

None of the studies mentioned above identified a single factor that can consistently predict koala leaf preference either across eucalypt species or between individual trees within a species. A series of recent studies with different approaches has been more successful in determining the chemical characteristics that affect the quality of foliage as koala food.

Pass *et al.* (1998) used a process of bioassay-guided fractionation of extracts from browsing susceptible and resistant individuals of *E. ovata* to identify Macrocarpal G, a formylated phloroglucinol derivative (FPC), as the specific compound responsible for resistance to herbivory by the common ringtail possum. Lawler *et al.* (1998*a*) subsequently investigated the role of this (and related compounds) in determining the acceptability of foliage of *E. ovata* and *E. viminalis* to koalas and ringtail possums. They measured intake of foliage from individual trees in no-choice experiments, and related intake to several measures of leaf chemistry, including FPC concentration. That study showed that variation in intake was closely correlated with the concentrations both of FPCs and 1,8-cineole. Lawler *et al.* (1998*b*) showed that another FPC, jensenone, acts by triggering an emetic response. Lawler *et al.* (1999) subsequently demonstrated and manipulated a dose-dependent conditioned food aversion in these species, where the animals associated the concentration of the terpene cineole in their diet with the post-ingestive effects of jensenone. As terpenes and FPCs are common in the foliage of so many eucalypt species eaten by koalas, and their concentrations have been shown to be correlated in several species (Lawler *et al.* 1998*a*, 2000), it seems that the 'learning through foraging consequences' model of diet selection may provide a useful framework for understanding koala feeding.

The key to these studies' success in identifying the role of FPCs was the focus on variation between individual trees and the measurement of a specific chemical rather than broad groups of chemicals, such as 'terpenes' or 'tannins', which comprise multiple components of varying structure and potency as potential antifeedants (e.g. Zucker 1983). Their antifeedant effect had not been detected previously because the standard assays used to measure 'total phenolics' use polar solvents, which do not extract non-polar phenolics such as the FPCs (Lawler *et al.* 2000).

As FPCs have been identified in a large number of eucalypts (Takasaki *et al.* 1994; Ghisalberti 1996; Lawler 1998; Eschler *et al.* in press) it seems possible that they may be a major determinant of diet selection by koalas. Importantly, however, FPCs have not been identified to date in eucalypts of the informal subgenus *Monocalyptus*, which includes species known to be eaten by koalas, such as *E. obliqua*, *E. pauciflora*, *E. dives*, *E. macrorhyncha* and *E. radiata* (Eschler *et al.* in press). This suggests that other unknown factors may influence diet selection by koalas within this group.

Incorporating an understanding of 'good koala food' into models of koala habitat

The question 'what makes good koala food?' is important because food quality is argued to be a key determinant of the quality of koala habitat (Norton and Neave 1990; Melzer and Houston 1997). Nonetheless, it is not the only factor that influences habitat quality for koalas. Once we understand the nutritional basis of diet selection by koalas, we can begin to investigate other factors, including social factors and the availability and quality of food in space and time. We can also begin to tackle the question of how the nutritional properties of a forest can be determined at a landscape scale.

How do koalas respond to variation in their food resource?

When we consider how koala habitat varies at different scales – most particularly between individual trees, but also between young and old leaves, between species, between regions and temporally between seasons – many new questions arise. Is nutritional quality the primary reason that koalas use particular trees? Will koalas use only the most palatable trees in an area, or are trees equally favoured as long as they meet threshold requirements? How do weather, season, the age of the koala, the lactational status of the koala and so on affect the dietary needs and tolerance of koalas, and the quality of koala habitat? By considering seasonal variation at the scale of the individual tree, we can ascertain whether palatable and unpalatable trees respond differently to seasonal changes in conditions and how the availability of koala food is affected. We can also begin to consider how other factors, such as tree shape and size, and location of a tree in an animal's home range influences tree use. What effect does the social structure of a koala population have upon the use of individual trees? And, crucially, how does the spatial distribution of suitable koala food trees in a forest or woodland affect the habitat quality of a given area?

One can imagine many ways in which palatable and unpalatable trees might be distributed through a forest or woodland. Palatable trees might be clustered, they might be ordered along an environmental gradient, or they might be distributed randomly through the environment. In a preliminary study, Lawler *et al.* (2000) found palatability to be normally distributed amongst *E. polyanthemos* trees in an area of woodland near Queanbeyan, New South Wales, but did not identify any spatial pattern. The next step towards answering this question must involve a larger-scale study incorporating environmental variables. Having described the environment in terms of its palatability, habitat use by koalas can be recorded and observed in that context.

Koalas inhabit environments that vary dramatically in environmental conditions and vegetation associations, from coastal Victoria to the arid zone of central Queensland (Martin and Handasyde 1999). They also exhibit great variation in population density and home-range size, the latter ranging from 39.2 ha for females and 86.5 ha for males in central Queensland (Melzer 1995*b*) to 1.2 ha for females and 1.7 ha for males on French Island (Mitchell 1990*a*). It is important that models of habitat quality do not just consider population density but also include a measure of long-term population stability/viability and the production of young that succeed in becoming established and reproducing (Norton and Neave 1990). In this way the individual roles of food quality and availability in determining koala carrying capacity, as opposed to habitat quality, can be identified. It may be the case that the number and density of suitable food trees available to koalas in an area dictates koala carrying capacity, but that the degree to which those trees exceed the minimal quality requirements for koala food determines these other attributes of habitat quality. Areas containing very high quality foliage might be vital as sources of dispersing animals to maintain populations in surrounding areas.

Using nutritional factors to model koala habitat quality at the landscape scale.

Ultimately, if we are to understand how the quality and availability of koala food affects the quality of habitat available to this species across its range we must develop a model of koala habitat that considers these factors at the landscape scale. This is especially important if this information is to assist conservation efforts. Obviously, it is not feasible to analyse the foliage of

every tree growing in potential koala habitat, so the challenge is to develop general rules that allow predictions about the extent of individual variation in *Eucalyptus* populations and the resulting quality of the habitat for koalas. These rules might be based upon environmental attributes such as topography, climate, abundance of particular eucalypt species, altitude, and fire and logging history – examples of these sorts of models are those of Braithwaite *et al.* (1984), Cork (1992) and Bennett *et al.* (1991). Alternatively, it may be the case that regional variation in habitat quality is more strongly influenced by the genetic makeup of eucalypt populations, which may be unrelated to environmental variables. Perhaps most likely, however, is a situation where both types of factors have a role to play in determining the value of an environment as koala habitat. Thus, there is a need for studies that incorporate between-tree variation at scales broad enough to resolve these issues and allow the development of rules or sampling procedures for predicting habitat quality. Once we have this level of understanding, recent developments in remote sensing offer hope that important nutritional parameters will be able to be measured directly over broad areas.

Acknowledgments

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