

The role of nutrition in the conservation of the marsupial folivores of eucalypt forests

Ben D. Moore, Ian R. Wallis, Karen J. Marsh, William J. Foley

School of Botany & Zoology, Australian National University, Canberra 0200

Correspondence: Ben.Moore@anu.edu.au, phone: (02) 6125 2534

ABSTRACT

This chapter discusses the nutritional factors that determine the densities of arboreal folivores – principally the koala, greater glider, common ringtail possum and common brushtail possum – in eucalypt forests. We examine the subject on two scales. The first is a broad approach that relies on the pioneering work of Braithwaite and colleagues, who examined attributes of forests, particularly the nutrient status, in relation to animal abundance. Our second approach is a fine-scale one that relies on studies of captive animals to decipher the role of anti-nutritional factors or plant secondary metabolites in feeding decisions by arboreal folivores. The knowledge accruing from these studies enables us to better explore the feeding ecology of wild animals. If we understand why animals feed on particular trees we can then explore why they use trees that they do not feed from. Similarly, by knowing the secondary metabolites that influence feeding it is then possible to measure their concentrations along environmental gradients to expand our understanding of plant-animal interactions. By reviewing information on the food preferences of the species and combining this with our laboratory feeding studies, we argue that the marsupial folivores select fundamentally different diets. What separates the species most are their preferences to feed from trees within a particular eucalypt subgenus, something we trace to chemical differences.

In reviewing the state of our knowledge, we highlight many questions that remain concerning how the nutritional quality of foliage varies across Australian landscapes. Several technological advances offer great hope for investigating these questions in both the laboratory and in the field. These same techniques will prove invaluable in monitoring changes in the nutritional quality of eucalypt foliage resulting from human activities and as a result of climate change.

Key words: *Eucalyptus*, plant secondary metabolites, formylated phloroglucinol compounds, koala, greater glider, common ringtail possum, common brushtail possum, diet selection, *Symphomyrtus*, *Monocalyptus*

Introduction

The view that nutrition underpins the replacement and expansion of all animal populations is now widely accepted. However, there are relatively few examples in wild species that define the critical nutrients and critical periods of nutrient supply and even fewer examples that demonstrate a link between the conservation of vulnerable fauna and nutritional status. This is partly explained by the difficulties in measuring the food intake and diet composition of wild animals. Thus, there is little idea of the rates of intake of nutrients and of toxins – the key factors that define the nutritional status of animals. This, in turn, makes it difficult to predict how nutrition will affect populations. Consequently nutrition, although widely recognized and implicated in population dynamics, is rarely a discipline for managing and conserving populations.

There are exceptions: in the Eden woodchip area in southeastern NSW, Braithwaite *et al.* (1983; 1984) found links between geological parent materials, foliar nutrient concentrations and the abundance of arboreal marsupials measured during clear felling operations. This research, which followed the studies of Turner and Kelly (1978) and Turner *et al.* (1981) linking soil nutrients and vegetation,

indicated patchiness, whereby abundant populations of arboreal marsupials occurred only on sites with relatively fertile soils. Specifically, 63% of the arboreal marsupial fauna occurred in only 9% of the forest area (Braithwaite 1983). This prompted further research that also supported the existence of a nutrient threshold for arboreal marsupials (Norton 1987; Cork 1992; Pausas *et al.* 1995; Cork and Catling 1996; Cork *et al.* 1997). Below this threshold there are insufficient nutrients to sustain populations. Above the threshold, population densities presumably vary with other factors, such as the availability of nest hollows, the amount of toxic chemicals that trees produce in their foliage, predation and the constraints of social interactions between individuals and groups of animals. In this way, nutrition underpins our understanding of a variety of other factors.

The ideas of Braithwaite and co-workers were most influential in the forest conservation debates of the 1980s and 1990s in arguing for the protection of forests growing on nutrient-rich sites – something realised at similar times in other parts of the world (e.g. McKey *et al.* 1978; Waterman *et al.* 1988; Oates *et al.* 1990; Peres 1997). Recently, others have looked for ecological correlates of animal abundance in forest and woodland communities elsewhere in Australia

(e.g. Munks *et al.* 1996; Kanowski *et al.* 2001; McIlwee 2001). A theme common to many of the above studies is that foliar chemistry is important. The problem, though, is that the term “chemistry” encompasses the two main subjects of animal-plant interactions: that of chemistry as a provider to the animal of nutrients and that of chemistry as a provider to the plant of defensive (often toxic) chemicals. This presents the problem of how to gauge the nutritional value of an environment. It presents also much wider problems of how human activity, including human-induced climate change, might alter the nutritional environment.

The purpose of this chapter is to summarise our understanding of the nutritional ecology of the foliage-eating marsupials of eucalypt forests, with particular emphasis on southeastern Australia. This avoids a discussion of a range of species that inhabit the wet tropics and which deserve special consideration elsewhere. The first half of the review focuses on the abiotic factors, such as geological parent materials, soil nutrients, climate, elevation and topography, that influence populations of arboreal folivores over large areas. The second half concentrates on factors that play at finer scales – largely biotic factors, such as how the chemical attributes of an individual tree determine the feeding decision of a possum or a koala. The two scales are not mutually exclusive but this separation provides a useful way to organise information and ideas. While we emphasise some recent progress we also point to specific areas that require more study. It is fair to say that the origin of many of our thoughts lies in the research of Braithwaite and his co-workers. Their research raised a host of questions, such as whether geological parent materials determine the density of arboreal folivores in eucalypt forests in other parts of the country. However, before examining this hypothesis and the influence of foliar chemistry on animal populations, we first examine the marsupial species of interest.

The four arboreal folivores of southeastern Australia

The arboreal folivores of southeastern Australia are all marsupials. This review focuses on four of them whose diet is predominately eucalypt foliage. We refer to them variously as the eucalypt folivores or marsupial folivores and define eucalypt in the broadest sense to encompass the major eucalypt genera of *Eucalyptus*, *Corymbia* and *Angophora*. It is important to note that eucalypt taxonomy is dynamic and at least two recent, major classifications exist, those of Brooker (2000) and of Hill and Johnson (1991a; 1991b; 1995). We use the latter classification, in which the genus *Eucalyptus* is split into seven subgenera, the two largest being *Symphomyrtus*, which contains roughly 500 species (mainly gums, ironbarks and boxes) and *Monocalyptus*, with about 130 species (stringybarks, ashes, white mahoganies and peppermints). We also mention species of another major eucalypt genus – *Corymbia* (bloodwoods, spotted gums and ghost gums) but make no further mention of the dozen or so species of *Angophora*. Eucalypt taxonomy is also important from the folivores’ perspectives, and thus we use (M) and (S) to denote whether a eucalypt is a monocalypt or a symphyomyrt. Appendix 1 lists the scientific and common names of all the eucalypt species we refer to and indicates their subgenera.

The four marsupial species of interest are the koala *Phascolarctos cinereus* (6 - 15 kg), the greater glider *Petauroides volans* (0.6 - 1.7 kg), the common ringtail possum *Pseudocheirus peregrinus* (0.6 - 1.4 kg) and the common brushtail possum *Trichosurus vulpecula* (1.5 - 4.5 kg). Eucalypt foliage is a poor quality diet. Nevertheless, an attribute that these folivores share is that they all survive on a eucalypt diet. This leads to other similarities, notably a reproductive strategy featuring a long lactation that avoids the massive peak nutritional demands of reproduction endured by most mammalian species. Alone, these two similarities between the species suggest competition. But, the differences between the species are many. These include size and gross anatomical differences, like the gliding membranes of the greater glider or the prehensile tail of the ringtail. While the two possum species and the greater glider are strictly nocturnal, the koala shows limited activity during the day. The need for shelter differs among the species too. The greater glider and brushtail possum spend the daylight hours in nest hollows as does the ringtail possum, which is capable also of building nest-like structures called dreys, thus foregoing the need for hollows. In contrast, the large body size of the koala removes its need for specific shelter, but being heavy may limit its ability to forage beyond the reach of larger branches. This is not a problem faced by the ringtail possum and the greater glider, which frequently forage in the tops of trees. In contrast, the brushtail possum spends much time foraging on the ground.

Perhaps the most important differences, from a nutritional ecology perspective, are those concerning dentition, gastrointestinal morphology and physiology discussed in depth by Hume (1999). Again, there are similarities and differences. All species expose the ingested food to some degree of microbial digestion – a synergy resembling that found in the domesticated ruminants. This enables the animal to extract more nutrients from its food as well as benefiting from the products of microbial metabolism and sometimes from microbial detoxification of toxins that are naturally present in leaves. In this respect, the ringtail is extreme. Like the greater glider and koala, it overcomes the paucity of nutrients in its diet by separating the nutrient-rich small particles in its gut from the coarser particles that contain fewer nutrients. However, while all of these species expose these fine particles to more digestion, the ringtail, through a phenomenon known as caecotrophy, re-ingests them directly from the cloaca, enabling it to gain nutrients – particularly microbial amino acids that it would otherwise lose. In summary, while the four species must tackle the same problem – obtaining nutrients from a relatively poor food resource, they differ in many ways in the solutions they have evolved.

It was this suite of differences that prompted Smith and Ganzhorn (1996) to suggest that eucalypt folivores achieve niche partitioning by vertical separation, rather than by evolving specific means to detoxify or tolerate plant chemicals that have a negative impact on food quality and thus achieving dietary specialisation. In other words, variation in body size and physiological adaptations for processing leaves with differing ratios of protein and fibre could explain most of the habitat differences. This

interpretation seems premature without first examining the diets of the four arboreal folivores with respect to the eucalypt species they select, whether selection occurs for individual trees within a species and whether these trees vary chemically.

What do the arboreal folivores eat?

One might expect, given the prominence of eucalypts in the Australian landscape and of the animals in wider culture, that we would know what arboreal folivores eat. To some degree this is true but there are many gaps in our knowledge. Recently, while compiling a list of the foods of these species, we were surprised by the paucity of information, particularly on the diets of greater gliders, ringtail possums and brushtail possums. The same can be said for the preferences of wild koalas but the many feeding studies on captive animals presents a much clearer picture of their preferences than we have for the other species. The fact that it is difficult to observe an animal feeding in trees at night probably explains our poor understanding of the dietary preferences of these animals in the wild. It also explains why radio-telemetry studies that generate information on tree use then become a surrogate for feeding observations. However, folivores may use trees for purposes other than feeding, and thus these surrogate data are unsatisfactory and may confuse our understanding of the nutritional ecology of arboreal folivores.

The four marsupial folivores rely on eucalypt foliage to differing extents, with the greater glider and koala being most reliant and the ringtail possum and brushtail possum being the least reliant (Cork and Foley 1997). These latter two species differ in their degree of folivory, with the ringtail possum relying on foliage much more than does the brushtail. Second, the marsupial folivores specialise to differing degrees on young and old foliage. Finally, all four species differ in their preferences for particular eucalypt species, which is likely to be linked to preferences for particular eucalypt subgenera, as summarised in Figure 1. A consequence of these trends is that we should not expect the distribution and abundance of each of the marsupial folivores to vary in the same way along ecological gradients. Furthermore, the nutritional factors that determine population sizes and dynamics are complex. With these trends in mind, we review our understanding of what food quality means for a eucalypt folivore.

How is habitat quality for folivores affected by the nutritional quality of foliage?

There are three aspects to this question that require different approaches. At the broadest scale, ecologists can measure animal abundance over a large area and then identify correlates – the approach that led to the formulation of the nutritional hypothesis discussed below. Considering the question at the scale of individual animals rather than populations, ecologists can observe animals feeding and try to explain their preferences. This may involve the collection and analysis of scats, which is a sound technique for identifying the species of eucalypt that a folivore eats (Ellis *et al.* 1999) but it will not identify a folivore's preferences

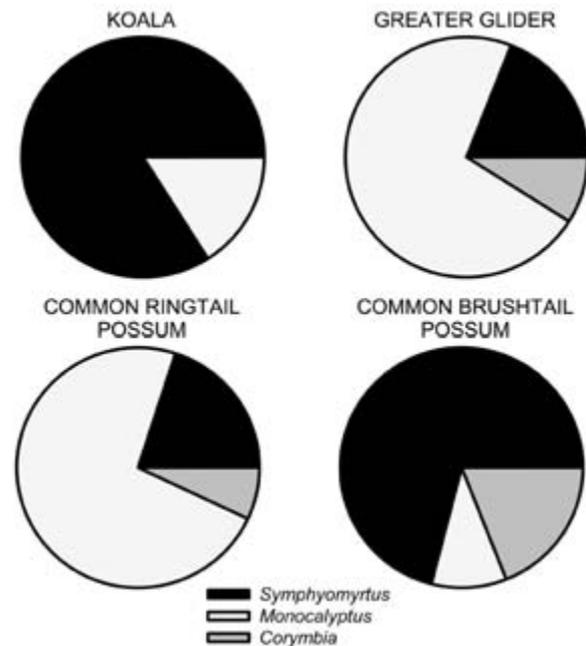


Figure 1. Proportion of eucalypt species belonging to three major taxa that represent major components of the diets of the koala, the greater glider, the common ringtail possum and the common brushtail possum. For koalas, *Symphyomyrtus* also includes *E. microcorys*, the sole representative of the subgenus *Nothocalyptus*.

for individual trees within a species. Finally, to collect detailed information about folivores' preferences for species or individual trees within a species, and the chemical basis for these preferences, experiments with captive animals are needed. This approach may even involve feeding studies with artificial diets containing chemical components extracted from eucalypt leaf.

The nutritional hypothesis

In their study of the animals observed by logging teams during "clear felling" of more than 5000 ha of eucalypt forest, Braithwaite and his co-workers (Braithwaite 1983; Braithwaite *et al.* 1983) found a concentration of animals, principally greater gliders, in 9 of the 22 vegetation communities. These communities tended to grow on fertile soils derived from the same geological parent material – Devonian intrusives. The communities included, in various associations, the following eucalypts: *E. fastigata* (M), *E. obliqua* (M), *E. nitens* (S), *E. fraxinoides* (M), *E. elata* (M), *E. radiata* (M), *E. dalrympleana* (S), *E. dives* (M), *E. ovata* (S), *E. cypellocarpa* (S) and *E. globulus maidenii* (S). A principal components analysis (PCA) that included the basal area of eucalypts considered of high nutritional quality along with an assortment of other habitat measures, including fire history, density of den trees and the numbers of trees in various age classes, produced principal components that accounted for 21-76% of the variance in population density of the different marsupials. In all cases, the nutrient status of the foliage was the key to explaining variance. In other words, the key eucalypts tended to produce foliage with high concentrations of nutrients (nitrogen, phosphorus and potassium). The principal components explained more variation in densities of greater gliders than other species, possibly because there were more data for that species.

Moving on from the nutritional hypothesis

Braithwaite's research in the southeastern eucalypt forests of NSW posed as many questions as it answered but most importantly it provided the central hypothesis for several later studies – that the nutrient content of foliage explained the distribution and abundance of arboreal folivores. In many cases these studies provided the first information that ecologists need to answer some of the important questions that Braithwaite's research raised:

1. Do similar relationships between soil parent materials and soil and foliar nutrient concentrations occur in other parts of Australia? This is important because even the highest soil nutrient concentrations in the southeastern forests are relatively low (phosphorus = 0.02 – 0.2 mg.g⁻¹ and nitrogen = 0.4 – 3.3 mg.g⁻¹). By comparison, the corresponding values in a similar study of arboreal folivores in north Queensland (McIlwee 2001) were 0.05 – 1.14 mg.g⁻¹ (phosphorus) and 0.77 – 3.02 mg.g⁻¹ (nitrogen).
2. Do nutritional gradients always largely explain the distributions and densities of arboreal folivores?
3. Are populations of marsupial folivores other than greater gliders similarly affected by variation in soil and foliar nutrient concentrations?
4. What role, if any, do toxic or 'anti-nutritional' plant secondary chemicals have in determining the distributions and densities of arboreal folivores?

We cannot offer clear and concise answers to these questions so we first consider what we know of the links between forest characteristics, such as fertility, and populations of each of the arboreal folivores.

Greater Gliders

Norton (1987) compared greater glider populations in three forest types growing on poor soils in Morton National Park with those residing in a more productive forest in Wadbilliga National Park. He found no greater gliders in the poorest forest at Morton. However, the population density in the intermediate forest type at Morton was equivalent to that at Wadbilliga, whereas the best site at Morton had the highest densities of any of the sites. These results support Braithwaite's observation of a nutrient threshold, above which population densities are highly variable. Despite the differences in population densities, Norton found that the population at Wadbilliga was more fecund than that at Morton, perhaps indicative of a nutrient threshold for reproduction. Nearby, at Kioloa State Forest, Davey (1989) found that the densest populations of greater gliders occurred in vigorous stands of high-nutrient eucalypt species providing abundant foliage biomass in the upper canopy.

In north Queensland, greater gliders preferred forests with *E. acmenoides* (M) and *C. citriodora*, both of which were common at the low end of a fertility gradient (McIlwee 2001). McIlwee found low densities of greater gliders in dry areas, in tall forests on high nutrient soils, at sites with low or high community foliar nitrogen concentrations and where tree species diversity was low. A high diversity

of species is thought to be important for greater gliders because it is most likely to provide a constant supply of young foliage or flower buds. Interestingly, tree species richness is often highest on soils of intermediate rather than of high fertility (Austin *et al.* 1996).

Common ringtail possums

It is more difficult to associate the abundance of ringtail possums with soil nutrients. They are absent or found at low densities on low nutrient soils in north Queensland (McIlwee 2001). However, densities at more fertile sites are variable, which is again suggestive of a nutrient threshold. Some of the highest densities of ringtail possums occur in *Leptospermum* growing on sand (Pahl 1987). High-density populations are common too in tick bush *Kunzea ambigua* and giant honey myrtle *Melaleuca amillaris* heathlands growing on similar substrates on the far south coast of NSW (e.g. Bournda National Park, Ian Wallis pers. obs.), however this may not indicate that foliar nutrient concentrations are low.

Common brushtail possums

Brushtail possum densities increase along soil fertility gradients. That said, this species is generally associated with drier sites (Owen and Thomson 1965; Davey 1989; Bennett *et al.* 1991; Johnson *et al.* 2001; McIlwee 2001).

Koalas

There is much more information on what constitutes suitable habitat for koalas than there is for the other arboreal marsupials. It seems widely accepted that "good koala habitat" occurs on fertile soils supporting particular favoured food species (Cork *et al.* 1990; Norton and Neave 1990; Lunney *et al.* 2000). It has also been suggested that the palatability of some koala food species, such as *E. punctata* (S), *E. agglomerata* (M), *E. tereticornis* (S) and *E. viminalis* (S) depends on the nutritional adequacy of the soil (Phillips and Callaghan 2000; Phillips 2000). There are exceptions, however, and other factors also influence the quality of koala habitat (Cork *et al.* 2000).

Koala populations of varying density occur on soil types ranging widely in fertility. There is ample evidence that there were still large populations of koalas in the Bega and Towamba Valleys in southern NSW in the second half of the nineteenth century (Lunney and Leary 1988; Reed and Lunney 1990). According to the Bega News (10/11/1865; cited by Reed and Lunney 1990) "it was possible to catch a Koala or Native Bear in the main street of Bega". What is less certain is the type of forest they inhabited. Reed and Lunney suggested that the koalas depended on *E. tereticornis* (S), which was cleared from the fertile valley floor in the latter part of the 19th century. Chris Allen (pers. comm. 2003) contends that the koalas may have relied as much on *E. baueriana* (S), which was heavily targeted for fence posts. Whatever the case, a community survey of the surrounding Eden region (Lunney *et al.* 1997) found that the low density relic populations mostly occur in dry forest dominated by the low-nutrient eucalypt species that Braithwaite *et al.* (1983; 1984) associated with vegetation communities that supported low mammal densities.

One of the largest koala populations in NSW has been reported from the Pilliga scrub, where the sandstone-based soils are mostly highly acidic and of low fertility (Humphreys *et al.* 2001; NPWS 2001). The highest koala densities anywhere are found in *E. viminalis pryoriana* (S) and *E. ovata* (S) forests in Victoria, where overbrowsing can lead to severe defoliation of food trees and eventual population collapse. These forests typically grow on poor soils, including skeletal podzolised soils and solodic soils derived from siliceous sand (Ladiges and Ashton 1974; Lee *et al.* 1991; Martin and Handasyde 1999). It is important to note, however, that foliar nutrients in these trees are not especially low. This example illustrates that adaptation in eucalypts can disrupt the link between soil nutrients and koala nutrition.

The association between dense koala populations and eucalypts growing on fertile soils and gentle topography, especially drainage lines, may be driven as much by water availability as it is by nutrients. At such locations, trees experience minimal water stress because the soils are deep and water tables are shallow. Hindell and Lee (1987) found that koalas in Victoria's Brisbane Ranges strongly preferred *E. viminalis* (S) and *E. ovata* (S) growing in fertile soils along drainage lines, but argued that koalas were selecting their food partly for its water content. This interpretation is supported by the observation that many koalas moved into the manna and swamp gum stands during a drought in 1982–83 (Hindell 1984). Likewise, during a severe drought in south-western Queensland, Gordon *et al.* (1988) saw 63% of their study population die, with most survivors inhabiting gullies where trees still found water. In many environments, it may be the case that forests cannot support permanent koala populations without adequate water availability.

The relationship between parent materials and soil and foliar nutrient concentrations

A dominant theme when investigating the distributions of marsupial folivores is the relationship among geology, soils and trees. There are many examples in Australia where basaltic parent materials give rise to highly fertile soils. For example, the Dorriggo Plateau, areas of the New England Plateau near Guyra and the Atherton Tablelands have extensive areas of Tertiary volcanics (basalt and trachyte mainly) that are highly valued for agriculture. Examples like these suggest a close association between the fertility of soils and the nature of parent materials, but does this relationship hold for the spectrum of parent materials? Furthermore, can it be extrapolated to vegetation communities?

Kelly and Turner (1978) argued that in the Eden district of southeastern NSW soil nutrient concentrations could be predicted from a knowledge of their parent materials. A little further north, at Batemans Bay, Austin and Heyligers (1991) suggested that altitude, latitude and geology are the major environmental variables associated with the composition of vegetation in the region. This invites the questions of what is soil fertility? Givnish (1999) defined

soil fertility as the supply rate of nitrogen and the major cations per unit area and suggested that it results from a complex function of temperature, rainfall and substrate texture, chemistry, drainage and oxygenation. Given the tremendous diversity of events that occur between the initial syntheses of soils to the establishment of modern eucalypt forests, the relationship between parent materials and soil nutrients is tenuous. It is probable that parent materials affect soil structure in ways that are just as important to plants as their effect on soil nutrients.

Although numerous studies have identified relationships between vegetation communities, parent material and soil nutrient concentrations (e.g. Turner *et al.* 1978; Braithwaite *et al.* 1984), nutrition is only one of many important factors that determine plant species distributions. The relationships between these factors are always complex and usually highly variable making any understanding contentious. The established view, promoted by Beadle (1954), is that many parent materials in Australia form soils that are nutrient deficient, particularly in phosphorus, and that phosphorus concentrations limit the distribution of most eucalypts. In contrast, Adams (1996) argued that total concentrations of nutrients in either parent materials or in soils have little bearing on the distribution and growth of tree species. Instead, he argues that total soil nutrient concentrations are poor indicators of 'fertility' because they often do not reflect the availability of nutrients to plants. Rather, availability depends on plant adaptations and, above all, on the rates of nutrient cycling. Integral in nutrient cycling and accumulation are mycorrhizal fungi (Bonfante 2003). In almost all ecosystems, mycorrhizae capture nutrients from the soil, particularly phosphorus. With regard to the distribution of eucalypts, the truth probably lies somewhere between the views of Beadle and Adams as indicated by the research of Austin *et al.* (1983), who found that altitude, rainfall, and solar radiation, as well as geology, influenced the distribution of eucalypt species. In summary, parent materials and soil nutrient concentrations affect the growth and distribution of some eucalypt species, but there is ample evidence that climate, elevation and the availability of water are often more important factors (Margules *et al.* 1987; Noble 1989). To complicate matters further, it is known also that canopy herbivores, particularly outbreaks of invertebrates, can influence forest soil processes. The mechanisms for these effects include changes in nutrient dynamics caused by invertebrates depositing faeces and changes in the way that precipitation passes through the canopy (Ohmart *et al.* 1983).

While a change in parent materials may not alter the species of eucalypt growing in an area, it may influence the acceptability of those species to arboreal folivores. Perhaps the best example of this phenomenon comes from populations of koalas residing in habitats derived from either shale or sandstone near Campbelltown, southwest of Sydney (Phillips and Callaghan 2000). Not only were there more koalas in habitats derived from shale, but koalas preferred *E. punctata* (S) and *E. agglomerata* (M) when they grew on soils derived from shale but not when they grew on substrates derived from sandstone.

Eucalypt species vary widely in their tolerances of different soils. Some species are restricted to a narrow range of soil conditions, but many species, including examples with low, intermediate and high foliar nutrient concentrations, occur over a broad range of soil types (e.g. Ladiges and Ashton 1974; Braithwaite *et al.* 1984; McIlwee 2001). Often the key to this observation is the conservation of nutrients through nutrient recycling, which allows productive plant communities to exist on soils with very low nutrient concentrations. For example, on the Cooloola dune system in Queensland, *E. pilularis* growing on phosphorus-deficient soils derived from pure sand (Walker *et al.* 1981) reach the same heights and similar foliar nutrient concentrations to *E. pilularis* growing on other soils with nutrient concentrations an order of magnitude greater (Turner and Kelly 1981). While this is an extreme example of the poor relationship between soil and foliar nutrient concentrations, it does gain some support from the studies of Lambert and Turner (1983), Davey (1989) and McIlwee (2001). It also illustrates that whether or not foliar nutrient concentrations are primarily determined by soil nutrient concentrations, the reverse is also true (Fensham and Bowman 1995; Adams 1996). This fact is the result of litterfall and nutrient cycling, and the occasional influence of fire. This said, soil nutrient concentrations also affect other attributes of trees that are important to folivores. For example, the height, girth and projected foliage cover of trees can be limited by low concentrations of soil nutrients (Ladiges and Ashton 1974; Davey 1989; Givnish 1999; McIlwee 2001; Wardle 2002).

What is important: the nutrient concentrations in a species or the nutrient concentrations in a community?

Because most eucalypts grow in multi-species associations and many grow on a wide variety of soils, it is difficult to generalise about how soil nutrient concentrations influence foliar nutrient concentrations in individual species. This problem did not concern Braithwaite *et al.* (1984) who disregarded species and instead calculated community nutrient concentrations: the mean foliar concentration of each nutrient, weighted by the proportional total tree basal area for each species. These community values indicated that foliar nutrient concentrations increase with soil nutrient concentrations, a result since confirmed in other studies (Davey 1984; McIlwee 2001). Before we can use this relationship to explain patterns of folivore abundance, we need to ask a question that has largely been ignored - whether mean community concentrations of nutrients (and plant toxins) are of greater importance to folivores than are the concentrations of nutrients in particular, favoured food species. Implicit in the use of the community measure is an assumption that folivores forage at random (Cork 1992). However, the reality is that animals show preferences for particular species within communities and for individual trees within these species.

The positive correlation between community and soil nutrient concentrations indicates that nutrient-rich

species often grow on nutrient-rich soils. Nonetheless, exceptions occur that may be important to folivores. For example, McIlwee (2001) found that although *C. citriodora* was abundant only at the low end of the fertility gradient in his study, it possessed the highest concentrations of foliar nitrogen and was strongly associated with greater gliders.

How do elevation and rainfall affect the nutritional quality of folivore habitat?

It is strikingly apparent, over a wide geographic range, that greater gliders are more common at higher elevations (Braithwaite 1983; Brown *et al.* 1987; Opie *et al.* 1990; Bennett *et al.* 1991; Kavanagh and Bamkin 1995; Braithwaite 1996). Indeed, Kavanagh and Bamkin (1995) concluded that elevation and predominant vegetation community were better predictors of animal occurrence than was geology. There may be a physiological explanation for this finding. Greater gliders (unlike most animals, which have thermoneutral zones covering several degrees) have a thermoneutral point at 20°C (Rübsamen *et al.* 1984). If the ambient temperature is higher than 20°C, greater gliders must expend energy and considerable water to cool themselves. Temperatures will generally exceed this point more at lower than at high elevations. Another likely explanation for the occurrence of greater gliders at higher altitudes is that this coincides with the occurrence of suitable forest communities or that land clearing has removed suitable habitat at lower altitudes (Braithwaite 1996). Braithwaite (1996) suggested a nutritional explanation for this pattern: where nights are cold relative to the days plants metabolise less photosynthate than do plants that experience warmer nights. Hence, the foliage available to nocturnal folivores may be more nutritious at higher altitudes.

Braithwaite *et al.* (1983) did not discuss the role of rainfall in the trends they observed, probably because climatic modeling packages were much less powerful then than they are now. Greater gliders have since been shown to be associated with high rainfall and wetter forests across their geographic range (Davey 1989; Bennett *et al.* 1991; Kavanagh and Bamkin 1995; McIlwee 2001). As for elevation, it is difficult to interpret the direct effect of rainfall on foliar nutrition, owing to its link with both soil fertility and species composition.

In conclusion, it seems that densities of arboreal folivores are influenced by geologic parent materials, soil nutrient status, elevation, topography, floristic diversity, rainfall, history of land clearing and no doubt by interactions among these factors. Although there have been some successful attempts to model the density of arboreal folivores in certain habitats (e.g. greater gliders in the montane ash-type forests of Victoria, Lindenmayer *et al.* 1990; 1995), evidence suggests that accurately predicting the presence and density of arboreal marsupials is currently precarious and will be for the foreseeable future. Further, to apply predictions at an appropriate scale for conservation purposes will require technology, such as remote sensing, supported by field survey work.

What defines food quality for marsupial folivores?

The conclusion drawn from a substantial body of literature is that concentrations neither of foliar nitrogen nor any other nutrient have ever provided a simple explanation for feeding decisions by marsupial folivores. This is not surprising. The concentrations of some nutrients in eucalypt foliage, like those of potassium and phosphorus, typically exceed the requirements of most mammals (Cork and Catling 1996). Alternatively, foliar nutrient concentrations may be correlated with other properties of foliage that determine whether folivores can obtain the nutrients they need for maintenance and reproduction. These other properties may include concentrations of indigestible fibre, the degree of sclerophylly or 'toughness' of leaves, the availability of digestible sources of carbohydrate and lipid and the concentrations of chemicals that deter herbivores. Foliar nutrient levels may simply reflect the productivity of a forest ecosystem, and thus the amount of foliage, particularly young foliage, that is available. It seems, whenever we go spotlighting, that someone raises the question: why, with all this food available, isn't there an animal in every tree? This shows how easy it is to assume there is abundant food for folivores, while evidence suggests that there is not.

Marsupial folivores and eucalypts have a long association. In this time both the trees and the marsupials have evolved a complex physiology to overcome life in an environment where nutrients are limiting. The adaptations of the trees include a variety of measures to protect the nutrients they accrue. Likewise, the marsupials have adapted to overcome the barriers that trees impose and to minimise their losses of key nutrients.

To demonstrate that there is no simple link between nutrients and diet selection by marsupial folivores we briefly review some of the evidence using nitrogen and digestible energy as key indices.

Nitrogen

Nitrogen was often thought to be the key to explaining diet selection by arboreal folivores (White 1993). The association between marsupial folivore densities and mean community foliar nutrient concentrations (nitrogen, phosphorus and potassium) gave this theory a glimmer of hope (Braithwaite *et al.* 1983). As a result it spurred much research, both in the field and with captive animals, with nitrogen as the focus. A series of experiments by Hume and co-workers detailed the low requirements for nitrogen (between 250 and 550 mg.kg⁻¹.d⁻¹ of truly digestible nitrogen, see Hume 1999) in arboreal folivores. This led Cork (1986) to argue that koalas can probably cope with foliage containing as little as 1% nitrogen on a dry matter basis. Our experience suggests that this is at the lower end of the range for eucalypt leaf, for which dry matter typically contains 0.8 - 2%. Thus, we expect that nitrogen concentrations alone would rarely restrict marsupial folivores – at least for non-lactating animals (Chilcott and Hume 1984b; Cork 1986; Foley and Hume 1987b; Cork and Catling 1996). While it seems possible

that there may be a threshold concentration for available nitrogen, below which animal numbers fall abruptly, nothing suggests that animal numbers should increase abruptly for increments above the threshold. This past research on nitrogen probably oversimplifies the picture because recently DeGabriel *et al.* (2002) pointed out that the arboreal folivores (with the exception of the ringtail possum that practises caecotrophy) cannot use nitrogen directly and instead have a requirement for amino acids. Thus, any discussion of nitrogen assumes that if foliage contains enough nitrogen for an animal then it also meets its amino acid requirements. However, DeGabriel's work indicated that brushtail possums were averse to certain free amino acids. Further research should focus on the link between the high proportion of free amino acids in eucalypt foliage (Journett and Cochrane 1978) and the apparent reluctance of possums to eat synthetic diets containing free amino acids.

The results from field observations are complicated. For instance, greater gliders sometimes show strong selection for tree species with high concentrations of nitrogen, such as *E. viminalis* (S) and *C. citriodora* (Norton 1987; Kavanagh and Lambert 1990; McIlwee 2001; Wormington *et al.* 2002). However, they also show strong associations with species possessing remarkably low nitrogen concentrations, like *E. acmenoides* (M), *E. andrewsii* (M), *E. globoidea* (M) and *E. consideniiana* (M) (Griffith 1973; Henry 1985; Norton 1987; Comport *et al.* 1996; McIlwee 2001).

Perhaps the most conflicting story of all concerns *E. consideniiana* (M). Greater gliders are absent or at best present in very low densities in forests containing this species (Recher *et al.* 1980; Braithwaite 1983; Braithwaite *et al.* 1984; Henry 1984). It is a species from the poorest forest types in Braithwaite's study and, not surprisingly, contains little nitrogen (e.g. 0.7 - 1.1% Braithwaite *et al.* 1983; Marsh *et al.* 2003a). Even so, at one of Norton's (1987) sites greater gliders preferred it (although this may have been an atypical site). Likewise, captive ringtail possums not only eat *E. consideniiana* but also gain weight on it (Marsh *et al.* 2003a) and it is a secondary koala food species in NSW (NPWS 2003). Is it possible that something else, like the availability of nest hollows, limits greater gliders in forests that include *E. consideniiana*?

There is less information on ringtail and brushtail possums. Cork and Pahl (1984) made a comprehensive effort to associate foliage selection to nutritional properties in ringtail possums near Melbourne, but found no link between selection for eucalypt species and nitrogen, nor any other measured nutritional property of foliage. In contrast, brushtail possums near Canberra preferred fertilised eucalypt seedlings, which apart from containing more nitrogen and soluble sugars, also had less fibre and tannins (Landsberg 1987).

The evidence is similarly mixed for koalas. Hume and Esson (1993) reported that captive koalas across New South Wales preferred foliage that had higher ratios of nitrogen to fibre and to condensed tannins. Similarly, Ullrey *et al.* (1981) reported that the preferred foliage of koalas at San Diego Zoo had more nitrogen than

did the rejected foliage, which prompted Degabriele (1981; 1983) to suggest that nitrogen limited koala populations. Pahl and Hume (1990) reported that captive koalas accepted leaf whose dry matter contained more than 1.8% nitrogen. This is higher than much of the foliage eaten by wild koalas and much higher than the 1% threshold for nitrogen suggested by Cork (1986). Extensive feeding trials with *E. ovata* (S), *E. viminalis* (S) and *E. globulus* (S) have not identified any effect of nitrogen concentrations in determining intraspecific variation in palatability (Moore *et al.*, submitted). While nitrogen concentrations are high in most primary koala food species, they are moderate or low in many secondary species (e.g. *E. punctata* (S), *E. consideriana* (M), *E. longifolia* (S), *E. agglomerata* (M), *E. globoidea* (M)).

A further complicating factor is that most folivores prefer young foliage. Young foliage generally has substantially more nitrogen than do mature leaves, but they also contain less fibre and more water and soluble sugars, and are easier to chew. This is further evidence that a combination of factors determines which leaves folivores select.

Energy

As for nitrogen, marsupial folivores display numerous anatomical, physiological and behavioural adaptations that minimise their energy requirements, emphasising the limiting nature of energy. For example, marsupials including the koala and the ringtail possum may extend their lactation period to prevent the energetic requirements exceeding availability from a eucalypt diet (Munks and Green 1995; Krockenberger *et al.* 1998). This suggests that knowing the energy available from foliage might provide further insight into diet selection by marsupial folivores. Not only does eucalypt foliage contain little protein, it also contains little metabolisable energy. Thus, it is difficult to know what limits folivores first (Hume 1999). Furthermore, the concentrations of nitrogen and digestible energy are related. As a leaf matures, the proportion of structural material, which is rich in fibre but poor in nitrogen, increases (Robbins 1983). Thus, by selecting young foliage, an animal is likely to increase its ingestion of both nitrogen and digestible energy.

Unlike nitrogen, there is no simple and meaningful measure of the available energy content of foliage. The total or gross energy content does not vary much, but the digestible energy varies enormously. Unfortunately, measuring digestible energy intake is a slow process requiring feeding experiments with captive animals. These measures can be done in conjunction with nitrogen digestibility experiments and they may yield interesting results. For example, in studies with ringtail possums, Hume *et al.* (1996) found marked differences in both food intake and the digestible energy contents of *E. punctata* (S) and *E. haemastoma* (broad-leaved scribbly gum; M) relative to each other and between summer and winter. These differences greatly exceeded the small differences in the foliage suggested by chemical analyses and supports the finding of Cork and Foley (unpubl.) that the metabolisable energy content of eucalypt species may differ by as much as 47%. The difference in energy yield lies in the nature and digestibility of the structural

carbohydrates. For instance, a high concentration of pectins probably explained the high digestibility of fibre in *E. andrewsii* (M) foliage fed to ringtail possums (Chilcott and Hume 1984a). Incidentally, this again illustrates the complexity of feeding in marsupial folivores. *Eucalyptus andrewsii* (M) is a species with low foliar nitrogen content, but is highly favoured by greater gliders (Cork and Foley, unpubl.).

We know of only one study (Osawa 1993) comparing the concentrations of soluble sugars among eucalypt species. However, these sugars may account for a substantial proportion of the digestible energy in a leaf and may vary both between and within species. Eucalypts in cold areas increase cellular concentrations of soluble sugars as an adaptation to frost (Leborgne *et al.* 1995), again suggesting an interaction between foliar nutrients and the environment.

Plant secondary metabolites

Our discussion so far has considered how nutrient concentrations influence what marsupial folivores eat and where they live, but it has done this without considering the 'anti-nutritional' properties of foliage, in particular the role of plant secondary metabolites (PSMs). PSMs are chemicals produced by plants that do not play a role in their essential, or primary metabolic processes. Many PSMs defend plants from herbivores by acting as toxins or otherwise reducing the nutritional quality of foliage. Eucalypts are renowned for their diversity of PSMs, which work in a variety of ways. Some, like the cyanogenic glycosides and formylated phloroglucinol compounds (FPCs), limit an animal's feeding on certain individual trees. Other PSMs, like tannins, may reduce the nutritional value of foliage. Thus, the nutritional quality of a habitat may be strongly influenced by the types and amounts of PSMs in foliage rather than by the nutrient properties of foliage alone. More importantly, the differing preferences of the marsupial folivores for individual species of eucalypts, or even groups of eucalypts, probably reflect the animals' abilities to counteract specific anti-nutrients in that foliage while acquiring nutrients. This represents another method of niche partitioning for marsupials, resembling the chemical partitioning proposed by Ganzhorn (1988) for primates in Madagascar. In this section we discuss the major classes of eucalypt PSMs.

Phenolics

The phenolics is a large and diverse class of compounds that includes the tannins, and many other chemicals whose molecular structures contain an aromatic ring with an attached hydroxyl (OH) group – a phenolic ring. Although total phenolics may comprise over 20% of leaf biomass in eucalypts, we have a poor understanding of the individual compounds that make up this mass because these compounds are often difficult to extract, separate and quantify. Hence, determining total phenolics is a common method of analysis and results are usually expressed relative to the standard tannin (quebracho) used in analyses. Expressed in this way, eucalypt leaf may contain 600 mg of quebracho equivalents per gram of dry matter.

Other methods of analysis separate condensed tannins, hydrolysable tannins and non-tannin phenolics and some distinguish individual components. The problem with analyses of groups of similar compounds, such as total phenolics, is that they ignore the biological relevance of individual compounds contained within the group and must assume that all phenolics affect herbivory equally. But, as Zucker (1983), Lawler *et al.* (1999a) and Kraus *et al.* (2003) point out, the structures of individual phenolics are varied and probably relate to their biological function. Perhaps the main drawback of “total phenolics” is that it typically refers to compounds extracted with a polar solvent, which leaves many less polar compounds behind. Others are partly extracted by the solvent but do not produce colour in the Folin-Ciocalteu reaction and thus remain undetected (Marsh *et al.* unpubl.; Noel Davies, pers. comm. 2003). One such group is the formylated phloroglucinol compounds (Marsh *et al.* unpubl.), which are arguably the most important PSMs in the interaction between eucalypts and marsupial folivores. For this reason we discuss them separately.

Cork (1992) realised that PSMs influence the feeding ecology of arboreal folivores and so examined the effect at a landscape scale by measuring the ratio of various nutrients (nitrogen, phosphorus and potassium) to total phenolics in distinct forest communities. Over a broad geographic scale this approach proved no better than using leaf nutrient concentrations alone, mainly because the concentrations of nutrients and phenolics are negatively correlated both within (Lawler *et al.* 1997; Moore *et al.* in press) and between eucalypt species (Cork and Catling 1996).

Studies with captive animals, and some field studies too, failed to provide evidence that total phenolics affect feeding (e.g. Cork and Pahl 1984; Hume and Esson 1993). However, Cork argued for the use of nitrogen:phenolic ratios because of the possibility that absorbed phenolic constituents can affect nitrogen excretion through impacts on acid-base balance (Foley 1992). However, there is no evidence that excretion of acid loads created by detoxification of PSMs increased urinary nitrogen excretion but simply that nitrogen is excreted as ammonia rather than as urea (Foley 1992). Furthermore, most foliar phenolics are excreted as glucuronide conjugates rather than as glycine conjugates (McLean *et al.* 2003) thus avoiding any additional loss of N. Accordingly we see little utility in the use of nitrogen:phenolic ratios as an indicator of food or habitat quality.

Although measures of “total phenolics” are too imprecise to be very useful in understanding interactions between eucalypts and herbivores, certain subgroups of phenolics are of immense interest. One such group is the tannins, a large class of phenolic compounds capable of binding proteins and thus capable of affecting the protein metabolism of the animal. Other tannins, particularly hydrolysable tannins, may be absorbed by the animal and elicit toxic effects. Although theory suggests a negative effect of tannins, the experimental evidence is less convincing. For example, Lawler *et al.* (1998b) found no correlation between feeding and foliar tannin

concentrations, although Hume and Esson (1993) reported that koalas preferred foliage with a higher ratio of nitrogen:condensed tannins. Studies of ringtail possums are even less convincing in identifying a negative effect of tannins. For example, blocking the effect of tannins with polyethylene glycol (PEG) increased food intake by about 10% but had little effect on nitrogen digestibility (McArthur and Sanson 1991; Marsh *et al.* 2003a;b). This confirmed earlier work by Cork and Foley (unpubl.) who found that ringtails digested most of the nitrogen in eucalypt foliage, leaving no room for improvement. Some species, including the koala, ringtail possum and brushtail possum, have gastrointestinal flora that are able to degrade tannin-protein complexes (Osawa and Sly 1992), although the exact mechanisms and the value of this association remains unclear. However, brushtail possums appear to react differently to tannins than do ringtails. Brushtail possums eat more of the foliage and digest more of the dietary nitrogen when tannins are inactivated (Foley and Hume 1987a; Marsh *et al.* 2003a;b). These examples illustrate a complicated story that again suggests a chemical separation of the marsupial folivores.

Terpenes

Terpenes, another major class of PSMs, are widespread in nature, mainly in plants as constituents of essential oils. Their strong smell and their toxicity to other animals probably explain why they are thought to affect feeding by eucalypt folivores. One would expect terpenes to affect feeding because animals must detoxify them. Nevertheless, no studies have linked the tree species preferences of marsupial folivores to total oil yields. But, like total phenolics, this may be the wrong measure because Hume and Esson (1993) found that koalas preferred tree species whose foliage contained at least 2% oil and that was rich in monoterpenes and poor in sesquiterpenes. Still other studies have shown no clear effect of terpenes on diet selection by marsupials (Eberhard 1978; Southwell 1978; Zoidis 1992). More recently, Lawler *et al.* (2000) fed *E. polyanthemos* (S) and *E. sideroxylon* (S) to ringtail possums and showed that the amount of foliage eaten is inversely related to the concentration of terpenes, particularly cineole. However, when cineole is added to artificial diets, brushtail and ringtail possums eat far more than they ever could from foliage (Lawler *et al.* 1998b; 1999b). Further research showed that cineole is not the primary deterrent in foliage but that its concentration is closely correlated to the concentration of the highly potent feeding deterrents, the FPCs (Pass *et al.* 1998; Lawler *et al.* 1999b).

The marsupial folivores detoxify terpenes in different ways (Boyle *et al.* 1999). Koalas, greater gliders and ringtail possums produce extensively oxidised metabolites. This presumably minimises the cost of detoxification and has the added benefit of reserving other mechanisms, like the glucuronidation pathway, for detoxifying phenolics. In contrast, brushtail possums produce less oxidised metabolites from ingested terpenes and also conjugate some of the metabolites with glucuronic acid (Boyle *et al.* 1999; 2000a; 2000b; 2001). The excretion of glucuronic

acid may be energetically costly unless the animal synthesises it directly from the high concentrations of ascorbic acid it obtains from eucalypt foliage (Dash and Jenness 1985). Both ringtail possums and greater gliders maintain high levels of ascorbic acid in the blood when feeding on eucalypt foliage, while brushtail possums do not (Dash and Jenness 1985).

Cyanogenic glycosides

Many individual trees of at least 30 eucalypt species contain the cyanogenic glycoside, prunasin (Gleadow *et al.* 2003). When animals chew leaves containing prunasin, the endogenous foliar β -glucosidase splits the molecule into a sugar and the potent respiratory toxin, hydrogen cyanide. Cyanogenesis may be more widespread than realised because it varies between eucalypt species and also between seasons. For example, manna gums planted in WA produced cyanide only in the winter (Congreve and Betts 1978).

Some mammals tolerate high concentrations of cyanide. The golden bamboo lemur *Haplemur aureus*, from Madagascar, can ingest 12 times more cyanide than the theoretical lethal dose for an animal of its size (Glander *et al.* 1989). The tolerance of folivorous marsupials for cyanide is unknown but if cyanogenesis were widespread among eucalypts then one would expect to find resistant populations of folivores. Brushtail possums, at least, can recognise cyanide and avoid it (Clapperton *et al.* 1996). This may not be true of koalas because cyanogenic manna gum foliage was implicated in the deaths of large numbers of koalas at Melbourne Zoo during winters in the 1930s (Pratt 1937). However, it is also possible that cyanogenic glycosides explain why Victorian koalas in captivity refused to eat *E. nobilis* (S) from the Styx River in northern NSW, despite its apparent nutritional similarity to their customary food species, *E. viminalis* (S) (Pahl and Hume 1990). A high proportion of *E. nobilis* (S) from this site has subsequently been shown to be cyanogenic (Gleadow *et al.* 2003).

Formylated phloroglucinol compounds

In their search for specific compounds that might explain feeding by arboreal folivores, Pass *et al.* (1998) recognised the limitations of the correlative approach for linking PSMs with feeding. Instead, they adopted bioassay-guided fractionation, an approach that had proven successful in other plant-herbivore systems (e.g. Bryant *et al.* 1983b). This technique overcomes prejudices about which compounds are important for animals by continually testing extracts derived from foliage that the animals are known to reject. This procedure eventually uncovered a large and diverse group of compounds known as the formylated phloroglucinol compounds. The common feature they share is a molecular structure containing a benzene ring with both hydroxyl- (OH) and formyl- (CHO) groups. Many also possess terpene side-chains.

We now know that for many eucalypt species the concentrations of FPCs are normally distributed throughout a population (Lawler *et al.* 2000; Wallis *et al.* 2002). Some individual trees produce foliage with almost no FPCs and are readily eaten by animals. Others resist herbivory by producing foliage with high concentrations of FPCs, while in between is the full spectrum of FPC concentrations. In a long series of feeding experiments with captive animals we have shown that FPCs largely determine feeding by ringtail possums (Lawler *et al.* 2000), brushtail possums (Wallis *et al.* 2002) and koalas (Moore *et al.* submitted). We have not done feeding experiments to see how greater gliders respond to FPCs. The three folivores that respond to FPCs all respond differently. Ringtail possums seem to stop feeding at much lower concentrations of foliar FPCs than do brushtail possums or koalas. When offered foliage from *E. melliodora* (S), brushtail possums and koalas still ate some foliage even when it contained up to 50 mg of sideroxydonal per g (equivalent to 5%) of dry matter. In contrast, ringtail possums refused foliage with 15 mg of sideroxydonal per g of dry matter (Figure 2).

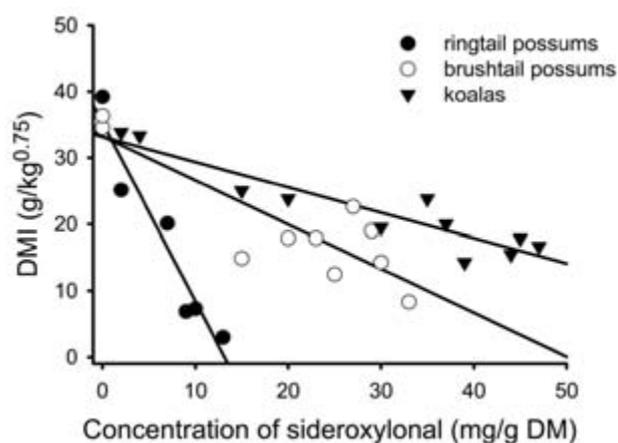


Figure 2. The relationship between the dry matter intake (DMI) of *E. melliodora* foliage and its sideroxydonal concentration for koalas, common brushtail possums and common ringtail possums. Body masses (mean \pm 1 s.e.): koalas = 6.8 \pm 0.9 kg, brushtail possums = 2.0 \pm 0.2 kg, ringtail possums = 0.9 \pm 0.1 kg. Ringtail possum data from Wiggins and Marsh (unpubl.); brushtail possum data from Wallis *et al.* (2002); koala data from Moore *et al.* (submitted).

There are two other important findings from these animal studies. First, in several of them (e.g. Lawler *et al.* 1998b; Wallis *et al.* 2002, Moore, submitted) we examined whether standard measures of leaf chemistry, including concentrations of total phenolics, terpenes, tannins and nitrogen, influence feeding or interact with FPCs. We found no relationships except for terpenes, the concentration of which was negatively correlated with feeding but positively correlated with the concentration of FPCs. Secondly, isolating FPCs and adding them to artificial diets for ringtail and brushtail possums confirmed the link between intake and FPC concentrations (Lawler *et al.* 1998a; b).

How do chemical differences between eucalypt subgenera affect their nutritional quality?

Ringtail possums seem more susceptible to FPCs than do brushtail possums or koalas, while brushtail possums seem more susceptible to tannins than do ringtail possums. Thus the nutritional quality of habitat may be strongly influenced by the types and amounts of PSMs the eucalypts contain.

The classification of eucalypts provides a particular insight into leaf chemistry and the feeding ecology of marsupial folivores. Eucalypts are classified by Hill and Johnson (1991a; b; 1995) into three main genera: *Eucalyptus*, *Corymbia* and *Angophora*. In turn, the genus *Eucalyptus* comprises seven subgenera, the two largest being *Symphomyrtus* and *Monocalyptus*. Our analysis of the diets of the marsupial folivores (Figure 1) has identified that the ringtail possum and greater glider eat mainly monocalypts, whereas the koala and brushtail possum are symphyomyrt specialists. This division coincides with a partition in PSMs (table 1). Symphyomyrts contain FPCs, whereas monocalypts do not (Eschler *et al.* 2000). Thus, even though FPCs are an important determinant of feeding, both koalas and brushtail possums tolerate limited amounts (Lawler *et al.* 1998b; Wallis *et al.* 2002; Moore *et al.* submitted). We would expect, on the basis of its preference for monocalypt foliage (fig. 1), that the greater glider would show a low tolerance of FPCs. As far as we know both monocalypts and symphyomyrts contain high concentrations of tannins, although we know little about the structure of these compounds. So, why are brushtail possums and, to some extent koalas, so reluctant to eat monocalypt foliage? We addressed this question by feeding brushtail possums two monocalypt species that are favoured foods of ringtail possums (Marsh *et al.* 2003a). The brushtails, all weighing about 2 kg, ate 17 g of dry matter per day, much less than the 60 - 70 g they need to eat to maintain weight in captivity. When the foliage was dipped in polyethylene glycol (PEG) to inactivate some of the tannins, the possums doubled their intake to 34 g. Unfortunately, we could not coat the leaf with enough PEG to inactivate the tannins that remained unbound to see if brushtail possums increase their feeding still further. Thus, we do not fully understand whether a characteristic of the tannins explains why brushtail possums do not like eating monocalypts.

Table 1: Distribution of plant secondary metabolites amongst eucalypt genera and subgenera.

Genus	Subgenus	Species (approx.)	Phenolics*	FPCs	Terpenes	Cyanogenic glycosides
Angophora		12	+		+	–
Corymbia		113	+	+/-	+	–
Eucalyptus	Eudesmia	18	+	+	+	–
	Nothocalyptus	1	+	+	+	–
	Symphomyrtus	504	+	+	+	+
	Monocalyptus	130	+	–	+	–

* Phenolics column does not include FPCs.

How do plant secondary metabolites vary across environmental gradients?

This question may be divided into two parts. The first considers how the distributions of monocalypts and symphyomyrts vary across environmental gradients – a subject of lively debate. The second part examines environmental influences on individual PSMs within a species, for which there seems little information.

Contrasts between symphyomyrt and monocalypt species

Symphomyrt and monocalypt species differ in several ways. From an ecological viewpoint, it is noted that although many eucalypts hybridise readily, hybridisation does not seem to occur between species from the different subgenera. Also, mixed stands of eucalypts tend to comprise species from the different subgenera (Pryor 1959). Austin *et al.* (1996) confirmed this rule, adding that eucalypt stands dominated by *Monocalyptus* only were more common than those dominated by *Symphomyrtus* only. Noble (1989) reviewed some of the finer differences between the subgenera and noted three differences that he regarded as indisputable. First, the subgenera differ in their leaf chemistry (see also table 1 and Lambert and Turner 1983). Second, compared to symphyomyrts, monocalypt species have less active root systems that lead to the trees being deleteriously affected by suboptimal conditions, particularly as they relate to soil moisture and temperature. Perhaps, as Pryor and Johnson (1971) suggest, monocalypts depend more on their mycorrhizal fungi than do symphyomyrts. Thirdly, the subgenera seem to differ in the establishment phase. These differences in early growth characteristics allow either to be the successful competitor in some situations. More recently, Stone *et al.* (1998) suggested that monocalypts suffer less damage from insect pests and other pathogens than do symphyomyrts.

From a nutritional perspective, and especially with regard to the nutritional hypothesis, the interesting comparisons concern nutrient concentrations, particularly foliar nutrients. Judd *et al.* (1996) assembled a database of the nutrient concentrations in 110 eucalypts growing in a variety of locations and environmental conditions. They concluded that symphyomyrts contained more calcium and manganese than did monocalypts but that there was no difference in the concentrations of nitrogen and phosphorus in tissue from trees of the two subgenera.

So, how do these differences between the subgenera influence their distribution and how does that affect arboreal folivores? Hughes *et al.* (1996a; b) found that while the frequency distributions of ranges of the two subgenera were similar, the mean and median geographic range sizes of symphyomyrt species exceeded those of monocalypt species. Furthermore, all species with ranges occupying more than 6% of the continent are symphyomyrts. Using rainfall data and distributions, they confirmed the suggestion of Florence (1982) that symphyomyrt species tend towards drier climates while monocalypts are generally restricted to the denser forests on the east coast and in the southeast and the southwest of Australia. The thoughts of Hughes *et al.* (1996a; b) agree with those of Noble (1989) who proposed a degree of specialisation within the monocalypts towards a tolerance of poorer soils in cooler more mesic sites. Hill *et al.* (2001) also suggested that symphyomyrts may be favoured by very high, and monocalypts by particularly low, soil manganese concentrations. It seems, then, that the trend in the distribution of the eucalypt subgenera fits the trends we mentioned earlier in the distributions of the arboreal folivores: brushtail possums and koalas are inclined towards drier places while greater gliders seem to inhabit wetter environments. In contrast, ringtail possums do not prefer a particular point on the rainfall gradient.

Environmental influences on plant secondary metabolites

Just as environmental gradients influence the concentrations of nutrients in eucalypt foliage, variation in PSM concentrations also occurs along environmental gradients. At any point, food quality depends on the tradeoff between the benefits to folivores of nutrients and the detriment to folivores of secondary chemicals.

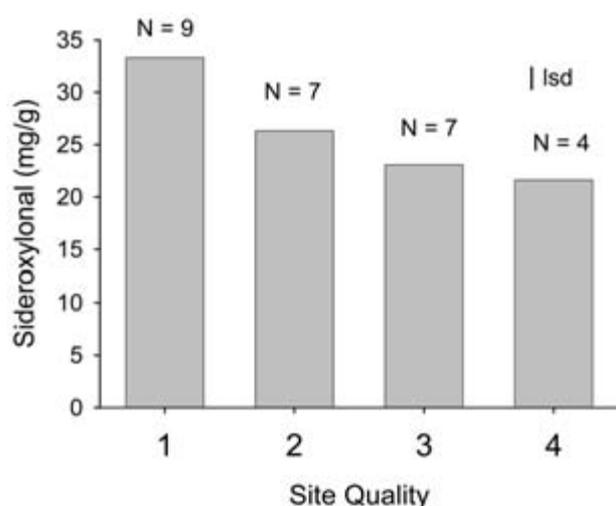


Figure 3. Predicted sideroxylylonal concentrations in tallwood *Eucalyptus microcorys* foliage from a linear mixed model for trees on the north coast of NSW growing at different site quality levels. Site quality is a measure of overall suitability for plant growth, where 1 is the highest quality and 4 the lowest. N = number of sites, lsd = least significant difference. Originally published in Moore *et al.* (in press).

Many theories of plant defence predict how plants defend themselves under different environmental conditions. Some, such as the carbon/nutrient balance theory and the growth-differentiation balance hypothesis describe the phenotypic response of plants to differences in nutrient availability and the favourability of conditions for plant growth. The carbon/nutrient balance theory (Bryant *et al.* 1983a; Lerdau and Coley 2002) predicts that PSM concentrations will be influenced by the carbon/nitrogen ratio in leaves. It says that this ratio will be higher, leading to increased concentrations of carbon-based PSMs (i.e. phenolics, terpenes and FPCs) and decreased concentrations of nitrogen-based PSMs (i.e. cyanogenic glycosides), in individuals of a plant genotype if they experience poor nutrient availability, high sunlight or elevated CO₂. This theory has been rejected by some ecologists because it often fails for carbon-based PSMs other than condensed tannins (Koricheva *et al.* 1998; Hamilton *et al.* 2001) and indeed, the evidence for eucalypts is mixed. Moore *et al.* (in press) found that concentrations of total phenolics, FPCs and terpenes were all negatively related to foliar nitrogen concentrations in *E. microcorys*. However, Lawler *et al.* (1997) found that total phenolic and condensed tannin concentrations increased, but terpene concentrations decreased, when *E. tereticornis* (S) seedlings were fertilised.

The growth-differentiation balance hypothesis (Herms and Mattson 1992) predicts that plants will produce higher concentrations of carbon-based PSMs when factors slow their growth more than their photosynthetic rate. This can occur because of cold temperatures and water or nutrient limitations. Again, in *E. microcorys*, Moore *et al.* (in press) found that concentrations of FPCs, terpenes and phenolics were all greater in trees at higher (colder) sites (fig. 4). Another theory also suggests that concentrations

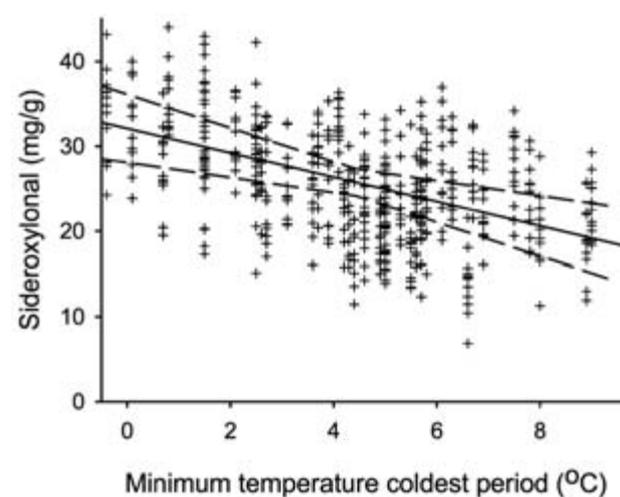


Figure 4. Linear mixed model (solid line) and observed values (crosses) describing sideroxylylonal concentrations in tallwood *Eucalyptus microcorys* foliage at 42 sites on the north coast of NSW that differ in the minimum temperature of the coldest week of the year. Dashed lines show the 95 % confidence interval. Minimum temperature decreases as elevation increases, so trees growing at higher sites had higher sideroxylylonal concentrations. Originally published in Moore *et al.* (in press).

of phenolic compounds (and possibly FPCs) should increase at colder sites. This is the photodamage protection hypothesis of Close and McArthur (2002), which suggests that the primary role of most plant phenolics may be to protect leaves from damage from solar radiation when cold inhibits photosynthesis.

Most other hypotheses concerning plant defence are evolutionary theories. That is, they make predictions about *evolutionary* responses of plants to conditions of resource availability, climate, competition and herbivory. As such, they concern the differences among plant species and between plant populations within species that have evolved in different environments. The resource availability hypothesis (Coley *et al.* 1985) predicts that plants in environments providing favourable growth conditions (adequate soil nutrients, water and sunlight) should contain lower concentrations of chemical defences than should plants in resource-poor sites. Like the carbon-nutrient balance hypothesis, this theory has its critics (e.g. Loreau and de Mazancourt 1999) and again, the evidence for eucalypts is mixed. In *E. microcorys*, FPC concentrations (which are the species' most potent deterrents of marsupial feeding) were higher, not lower, at high quality sites (fig. 3), while other PSMs were not affected by this gradient. Cork (1992), Cork and Catling (1996) and McIlwee (2001) found that concentrations of phenolics were higher in eucalypt species and communities with higher foliar nutrient concentrations growing on more fertile soils. However, in the first study, these relationships were weak and disappeared when examining individual components of the total phenolics. More importantly, total phenolics alone were unable to discriminate between forest communities described as favourable and unfavourable by Braithwaite *et al.* (1984).

One PSM known to have a detrimental effect on most animals is cyanide. That said, there is little more than circumstantial evidence of how marsupial folivores react to foliage containing cyanide, such as that of *E. cladocalyx* (S). Cyanide production in *E. cladocalyx* is strongly influenced by foliar nitrogen concentrations, with as much as 20% of the foliar nitrogen incorporated into prunasin. Fertilisation affects the concentration of prunasin in leaves, as does site fertility. Woodrow *et al.* (2002) reported that *E. cladocalyx* growing at a fertile site on the mainland of South Australia produced leaves with higher concentrations of both nitrogen and prunasin than did trees growing at a poorer site on Kangaroo Island, South Australia. Cyanogenesis in *E. cladocalyx* is also closely related to the availability of water: seedlings given limited water and trees growing at drier sites possess more prunasin (Woodrow *et al.* 2002). In this case we need to understand how animals respond to cyanide. Is there a threshold dose or is there a tradeoff? For example, if an animal ingests more protein it may be able to detoxify more cyanide by synthesising more of the detoxifying protein rhodanase (Gleadow and Woodrow 2002).

We have much to learn about how PSMs vary along environmental gradients. Even so, there is no doubt that the ways in which PSM concentrations vary among eucalypt species and among trees across the environment

are many and varied. There is a need for concurrent studies measuring variation of PSMs along environmental gradients and others to understand the effect of individual chemicals on arboreal folivores. In this regard, a key problem to solve is why koalas and brushtail possums refrain from eating monoclypts.

Extrapolating nutritional knowledge from the laboratory to wild populations

Animals need nutrients to sustain their life processes. These may be broadly classified as maintenance, thermoregulation, growth, activity and reproduction. Typically, experiments with captive marsupials restrict these life processes by housing mature, male or non-breeding female animals in warm rooms where they have free access to food and water and where activity is limited. In contrast, free-living animals respond to factors that captive animals do not experience – predation, climate, reproduction, growth, disease, social interactions, and particularly variations in the quantity and quality of food. All of these have associated energy costs, while growth and reproduction require the acquisition of a wide variety of nutrients. What is the point, then, of studying captive animals? Secondly, is it possible to extrapolate the nutritional knowledge attained from a few captive animals to the role that nutrition plays in free-living populations of animals?

The answer to the first question is that studying captive animals allows us to remove various confounding factors and ask simple questions that might then be related to wild populations. One such question that we have focused on is how brushtail and ringtail possums and koalas respond to wide-ranging dietary concentrations of FPCs. This work had its foundation in observations that some trees experience much greater herbivore damage than do nearby conspecifics (e.g. Geritz 1987; Hindell and Lee 1987, W. J. Foley unpubl.; Pahl 1987). The logical extension of these observations was to feed captive animals on trees known to vary in their concentration of FPCs. As described above, all three species are susceptible to these secondary chemicals but to differing degrees (Lawler *et al.* 2000; Wallis *et al.* 2002; Marsh *et al.* 2003b; Moore *et al.* submitted). Furthermore, especially in the case of brushtail possums, there was substantial variation in food intake that could not be explained by FPC concentration or by other measures (e.g. nitrogen content) and thus remained unexplained. By examining this residual variation it may be possible to identify other determinants of food intake. Perhaps the next phase of research with captive animals might be to ask how an increase in metabolic rate – induced through reproduction or exposure to cold – affects an animal's ability to cope with secondary chemicals.

This brings us to the second question: how do we translate our observations on captive animals to free-living populations of arboreal folivores? Apart from factors that directly affect the nutritional status of free-living animals, there are others that impinge on their life histories – notably social interactions and predator avoidance. In the case of arboreal folivores, this means that animals may use trees for a variety of reasons other than as food resources. Thus, a tree containing hollows may be both a den tree

and a food tree or it may be distant from feeding grounds, necessitating the animal to traverse many trees before settling in a feeding tree. Thus, observations of tree use are not always good indicators of food resources (Ellis *et al.* 1998; Logan and Sanson 2002). Instead, determining food resources requires detailed observations of radiotracked animals to categorise how individuals use each tree in their home range. Due to temporal variation in leaf chemistry, these observations need to be made in various seasons and probably over several years. This step is an enormous leap from demonstrating that FPCs influence the feeding decisions of captive arboreal folivores. Such complexity suggests that moving immediately from simple experiments with captive animals to trying to establish direct links between FPCs and the feeding decisions of free-living animals is inviting failure. An alternative approach is to seek intermediate steps, one of which is to understand the distribution of FPC concentrations in the foliage of individual trees in an area relevant to an animal – its home range.

One problem with field studies of chemical ecology, especially those covering areas as large as an animal's home range, is that they are soon constrained by the time and cost of large-scale chemical analysis. The home ranges of greater gliders and ringtail possums are typically <1 - >2 ha, brushtail possums usually range over 1 - 4 ha while koalas have widely varying home ranges (<1 - >100 ha). Eucalypt forests and woodlands contain more than 100 trees per ha so the scale of the chemical analyses needed runs into thousands of samples. One way of resolving this problem is to use near infrared reflectance spectroscopy (NIRS) – a rapid method of analysis, the principles of which were described by Foley *et al.* (1998). NIRS, which is now applied widely to eucalypt foliage, cannot be used in isolation as an analytical tool, but instead requires the support of conventional analyses. Briefly, if a sample is exposed to light in the near infrared wavelengths, then the chemical bonds in the sample determine the resulting reflected spectrum. These spectra can then be calibrated against reference values obtained by traditional analytical techniques to obtain equations for predicting chemical concentrations in samples whose spectra fall within the bounds of the calibration set. After developing the calibration equation, it is possible to analyse many hundreds of samples per day. Moreover, provided there are already calibration equations, a single NIRS scan yields a spectrum that can be used to predict the concentrations of several chemical components – e.g. nitrogen, amino acid and FPC concentrations. It can even predict functional attributes of foliage, such as how much of it an animal will eat (McIlwee *et al.* 2001; Wallis and Foley 2003).

Lawler *et al.* (2000) used NIRS to analyse the foliage of all of the *E. polyanthemus* (S) trees in the typical home range of a ringtail possum. They showed that both the sideroxylyonal concentrations and the potential dry matter intakes of the foliage by ringtail possums were normally distributed. They deduced that there were few trees that ringtail possums could eat freely and few that were so well defended that possums could not eat them at all. A similar survey by Wallis *et al.* (2002) of 150 *E. melliodora* (S) reached a similar conclusion. Both studies provide evidence that food trees

are patchily distributed within an animal's home range. The obvious implication of this conclusion is that while species of marsupial folivore may prefer certain eucalypt species, the presence of a particular species does not automatically consign the status of good habitat.

Now that we have some knowledge of the distribution of FPCs in natural eucalypt stands, it is possible to make predictions about the feeding decisions of animals. Evidence that FPCs influence feeding by free-living animals is only now being produced. In a study in north Queensland, Scrivener *et al.* (2004) measured a 6-fold range in the concentration of FPCs in the foliage of individual trees within a single eucalypt species. Although they measured tree use, rather than feeding, they did observe that brushtail possums avoided trees with high FPC concentrations. In contrast, some trees with low FPC concentrations were used heavily while others were not. Through a novel statistical process, the authors were able to show a relationship between tree use and FPC concentration.

The next step in this approach is to repeat the study, this time with feeding observations and at several sites to better understand the implications of habitat quality for arboreal folivores. For instance, we still do not know what makes good nutritional habitat for these animals and what the life history implications of good habitat are. However, we do know that population densities vary widely over distances of several km. In these places we might ask how many food trees an animal needs in its home range. Does it make any difference if the range contains mainly chemically defended trees with a few highly edible trees or if most trees contain low to medium concentrations of defensive chemicals? If so, how does this translate to measures of life history, such as reproductive output and longevity?

The only other study associating free-living arboreal folivores with FPC concentrations was the previously mentioned *E. microcorys* study of Moore *et al.* (in press). At 19 sites occupied by koalas on the NSW north coast, those trees with koala faecal pellets at their base were larger than trees without pellets, had significantly lower concentrations of cineole and tended to have lower concentrations of sideroxylyonal.

These studies both suggest that FPC concentrations may influence the distribution and abundance of marsupial folivores at landscape scales. But, apart from the need to examine feeding in relation to PSM concentrations in several populations of marsupial folivores, there is the need also to better understand the distribution of PSMs over entire landscapes. One way of doing this is by remote sensing, using airborne NIRS sensors, such as the Australian HyMap™ (Integrated Spectronics Pty Ltd), which collects 128 wavebands from 450 nm to 2500 nm. There are many problems to overcome to translate airborne spectra into meaningful information – in this case, spectra of foliage and then the chemical composition of foliage. Among the most difficult are removing atmospheric interference and background effects to leave so-called pure tree pixels. Even so, by collecting the spectra of 50 *E. melliodora* (S) trees with HyMap™ and by actually analysing the foliage from these trees, Huang

et al. (unpubl.) proved the potential of remote sensing for measuring the concentrations of both nitrogen ($r^2 = 0.79$) and sideroxylonal ($r^2 = 0.86$). These early results suggest that with further refinement it will be possible to map the nutritional habitat of arboreal folivores from the air.

The role of nutrition in conservation of the marsupial folivores

With an understanding of the role of nutrition and plant chemical defense in determining habitat quality for folivorous marsupials, we can start to question the impacts of forest management and other human activity upon the nutrition both of the forest and its fauna. Major sources of disturbance in Australian forests include forestry activities, such as harvesting and the replacement of natural forest ecosystems with hardwood plantations, and fire. Human activity may also affect foliar chemistry via 'nutrient pollution' and global climate change.

Throughout the following discussion, recall that increased availability of nutrients may increase the productivity and foliar nutrient (especially nitrogen) concentrations of eucalypts and that the depletion of soil nutrient reserves may have the reverse effect. The effects of these changes on PSM concentrations require further study. Concentrations of phenolics and possibly of FPCs are likely to decrease if foliar nitrogen concentrations increase, however the evidence for terpenes is contradictory (Lawler *et al.* 1997; Koricheva *et al.* 1998; Moore *et al.* in press). Increased foliar nitrogen should increase cyanogenic glycoside concentrations in plants that already possess them (Woodrow *et al.* 2002). The effects of changed nutrient regimes are less easy to predict in the long-term, i.e. over several generations of trees. Productivity may decline if nutrients are lost from an ecosystem at a faster rate than they can be replenished, but tree growth rates may slow and thus prevent changes in foliar nutrient concentrations. The general evolutionary response of eucalypt PSMs to changing resource availability is uncertain, however *E. microcorys* trees growing at higher quality (i.e. more productive) sites contain higher FPC concentrations (fig. 3.; Moore *et al.* in press).

Forestry activities

Logging activities displace surface soils causing a net loss in productivity (Florence 1996). Compaction of soil by heavy machinery reduces the potential for root growth and thus the potential for trees to acquire water and nutrients (Rab 1994). The long-term effects of these processes are unknown, but may have a bearing on the ecological sustainability of forestry operations (Florence 1996).

A large proportion of the forest biomass is removed by timber and woodchip harvesting, prompting the question of nutritional sustainability. If the nutrient capital of the soil is reduced over repeated harvesting cycles, it is possible that the nutritional quality of foliage and the productivity of the forest will decline. Most nutrients in forest ecosystems are contained in the soil and in below-ground biomass. Of the remainder, a higher proportion are found in the bark than in the woody bole. Consequently, nutrient losses to timber

harvesting represent a small proportion of the total nutrient pool and can be reduced by debarking logs on site (Hopmans *et al.* 1993). A greater loss of nutrients occurs when slash residue from logging operations is burnt, especially if the fire is intense, as is often the case when fires are used to create a seedbed after clear felling (Hopmans *et al.* 1993; Florence 1996). This is due to both volatilisation of nutrients and particulate loss in smoke. None the less, regrowth on both high and low-quality sites after burning is vigorous and no evidence exists for any adverse effect of logging or slash burning on the productivity of regrowth forest (Florence 1996). In terms of macronutrients, nutrient cycling appears to be resilient to nutrient losses from logging and fire over sufficiently long rotations, because nutrient losses are nearly or entirely balanced by nutrient inputs (Attiwill 1994). However, significant depletion of forest nutrient pools is most likely to emerge after several rotations over 200-300 years (Turner and Lambert 1986), so the long-term effect of these processes may not be known for some time.

Low-intensity and selective logging can also affect the nutritional quality of foliage by increasing the amount of sunlight reaching the remaining trees. A study in a dry deciduous forest in Madagascar found that logging that affected < 10% of the forest surface caused no change in leaf fibre concentrations but increased protein, sugar and condensed tannin concentrations. Because tannin concentrations leveled off at lower light intensities than did protein and sugar, the average leaf quality was improved and sightings of folivorous lemur species increased (Ganzhorn 1995). Harvesting of firewood (e.g. in the box-ironbark forests and woodlands of Victoria) is one example of low-intensity logging in Australia. However, its impact on the nutrition of marsupial folivores has not been assessed.

Nutrient pollution

Human activity has increased inputs of nutrients into most ecosystems. Both nitrogen and phosphorus are released into the atmosphere from the burning of plant materials and fossil fuels and from other pollutants. They may be transported over both short and long (up to a few thousand km) distances before being deposited (Newman 1995; Verhoeven *et al.* 1996; Bobbink 1998). In many ecosystems, nitrogen deposition leads to increased nitrogen availability and results in changes to the plant community as nitrogen-loving species are advantaged (Bobbink *et al.* 1998). In the northern hemisphere, chronic nitrogen deposition has been shown to cause declining productivity and greater mortality in some forest types (Fenn *et al.* 1998). In lieu of an unlikely reduction in emissions, management of this problem is probably only feasible in high-priority areas and on a limited scale (Fenn *et al.* 1998). Nutrients are also deposited by sewage runoff and stormwater from roads and urban areas. Past and continuing fertiliser application, sowing of exotic grasses and legumes and grazing has resulted in elevated soil nutrient concentrations on some land used for agriculture and forestry, and in areas to which they drain (Loneragan 1997; Costantini and Lcoh 2002; Jurskis and Turner 2002).

In most cases, elevated nutrient availability is likely to increase the nutritional quality of foliage, although we stress again that the response of PSMs is less predictable. While this might initially appear to be beneficial for marsupial folivores, it is almost certainly outweighed by the negative impacts of other processes. The higher nutritional quality of foliage leads to increased insect herbivory (reducing the availability of foliage to marsupials) and is believed to be a major cause of dieback (Landsberg 1990). Furthermore, the weedy and exotic species that replace the original vegetation will often not provide suitable foliage for specialised marsupial folivores (Low 2002).

Folivore 'overpopulation'

Sometimes, populations of marsupial folivores reach such high densities that defoliation of preferred tree species occurs, eventually resulting in tree death and partial ecosystem collapse. With koalas and ringtail possums, this occurs most commonly in stands of *E. viminalis* and/or *E. ovata* in Victoria and South Australia (Pahl 1985; Geritz 1987; Martin and Handasyde 1999). Brushtail possums have been implicated in dieback in the midlands of Tasmania (predominately of *E. viminalis*; Statham 1992), and of *E. polyanthemos* in the You Yang Ranges west of Melbourne (Low 2002). The devastating impact of brushtail possums on non-eucalypt foliage when introduced into foreign ecosystems, such as New Zealand and the Keppel Islands in Queensland, is also well known (Kerle 2001; Low 2002).

Many factors combine to allow marsupial folivore densities to reach these levels. These may include lowered mortality rates resulting from reduced hunting, predation and fire frequency; isolation of habitat preventing dispersal; and in some cases the availability of exotic food sources including improved pasture (Statham 1992; Martin and Handasyde 1999). However, the strong association with particular eucalypt species suggests that 'overpopulation' can only occur where the nutritional quality of foliage makes it possible. This prompts the question of whether human influence has affected the nutritional quality of foliage where overpopulation occurs or whether this is its natural condition. Jurskis and Turner (2002) suggested that reduced fire frequency since European settlement has allowed the development of denser, more mesic understoreys and led to elevated soil moisture, increased soil and foliar nitrogen concentrations and reduced soil temperatures. They argued that this process has triggered population increases and greater herbivory by koalas and insects, eventually leading to tree dieback and koala population collapse. Beyond a certain point, positive feedback drives the process, regardless of whether human activity changed the nutritional environment in a way that caused the initial rise of folivore populations. Heavily attacked trees respond to herbivory by producing epicormic growth that contains higher concentrations of nitrogen and sugar, higher water content and a lower proportion of fibre than typical adult leaf (Landsberg and Cork 1997). This encourages further herbivory, until eventually the tree's resources are depleted (Martin 1985).

Fire regimes

Fire is unquestionably a key element in Australian ecological processes. However, the question of whether or how humans should manage fire is a contentious issue. Fire has many impacts on marsupial folivores. Intense fires kill many animals directly and deplete the food resource for the survivors. They also initiate the development of tree hollows and cause changes to the floristic composition and biomass of the understorey, which particularly affect brushtail and ringtail possums. Thus, the nutritional consequences of fire management must be weighed up against all of these factors. The epicormic regrowth that eucalypts produce after fire is softer, contains more macronutrients and has a lower carbon/nitrogen ratio than adult foliage, and consequently experiences a greater level of insect herbivory (Steinbauer *et al.* 1998; Radho-Toly *et al.* 2001). This foliage is probably a superior food for marsupial folivores too, however no one has investigated how PSM concentrations respond to fire. Compared to adult foliage, young eucalypt foliage usually contains higher concentrations of all major PSMs (B. D. Moore unpubl., Landsberg and Cork 1997; Gleadow and Woodrow 2000). Therefore, we need to ask to what extent the improved nutritional quality of foliage can compensate for any increases in PSM concentrations.

The effect of regular prescribed burning will depend on its frequency and intensity. Burning cycles that are too short will cause an unsustainable loss of ecosystem nutrients (Florence 1996), leading to lower concentrations of foliar and soil nitrogen and depressed productivity (Raison *et al.* 1993). Florence (1996) concluded that an appropriate regime for the conservation of forest wildlife must incorporate a high level of diversity in burning frequency and intensity.

Plantation forestry

Monocultural eucalypt plantations account for an increasing proportion of Australia's forested area. Apart from a single age structure, these differ from most natural forest stands in their reduced species diversity and reduced phenotypic and genetic diversity within species. They also differ from other production and protected forests in that wildlife conservation is not a management concern. Seedstock for plantations is selected from individual trees and provenances possessing traits that are desirable from a plant breeding and timber-producing perspective. Because tree breeders select for fast growth rates and high productivity, the nutritional quality of plantation foliage is likely to be good. In fact, marsupial browsing is a major factor affecting the success of eucalypt plantations, particularly in Tasmania, where lethal control methods, such as 1080 baiting, are used. Perhaps by developing eucalypt plantations in which natural patterns of variation in chemical defense are replicated, a solution can be found that allows the coexistence of sustainable plantation forestry and marsupial conservation.

Climate change

Climatic variables determine the distribution of eucalypts and influence their chemistry. Thus it is pertinent to discuss how climate change may affect the nutritional resources of marsupial folivores. Under some scenarios of

climate change (recently reviewed by Hughes 2003), the nutritional limitations to the distribution and abundance of folivorous marsupials will change. The effects of future climate change on Australian ecosystems are complex, with considerable uncertainty in both the direction and magnitude of local temperature and rainfall responses. However, the CSIRO Climate Impact Group (2001) suggested that by 2030 most places would be 0.4 - 2.0°C warmer than they were in 1990. More rain will fall in places that predominantly receive summer rain, while places that receive winter rain will be drier. In *E. microcorys*, FPC concentrations are higher at cold sites (fig. 4., Moore *et al.* in press), so concentrations of these toxins may decrease as temperatures rise. More predictable is the continuing rise in concentrations of atmospheric CO₂, prompting several studies examining its effect on the composition of plant tissue. Studies of *Eucalyptus* (Lawler *et al.* 1997; Gleadow *et al.* 1998), *Acacia* (Evans *et al.* 2000) and of some rainforest genera (e.g. *Alphitonia*, *Flindersia*; Kanowski 2001) grown in glasshouses under elevated CO₂ showed decreases in foliar nitrogen with simultaneous increases in plant polyphenols and other refractory components. The resulting increase in the carbon:nitrogen ratio of the tissue may decrease its nutritional value.

Considering these effects along with the folivore distribution and foliar chemistry data gathered by Braithwaite *et al.* (1983) and Cork (1992) makes for a striking illustration of the potential effects of elevated CO₂ on fauna in the southeastern *Eucalyptus* forests (Figure 5). However, the effects identified in laboratory studies may be extreme. First, most of these studies were made with potted plants grown in artificial media and with plentiful nutrients, water and light. Hughes (2003) pointed out the importance of measuring the response to elevated CO₂ when these components are

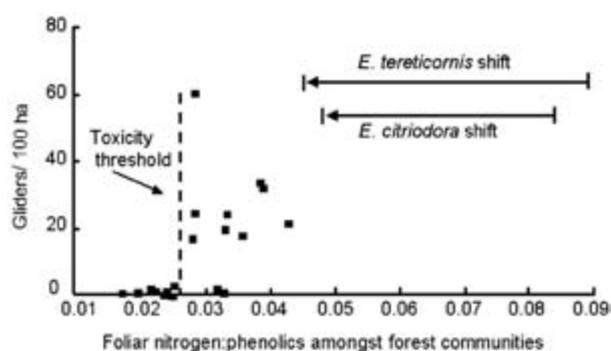


Figure 5. The possible effect of elevated CO₂ on habitat quality for greater gliders. The horizontal arrows show the shift in ratio of nitrogen:phenolics from seedling leaves of two eucalypt species grown in 350 ppm CO₂ to those grown in 800 ppm (Lawler *et al.* 1997). The plotted data show the relationship between greater glider densities and foliar nitrogen:phenolic ratios in eucalypt communities in SE NSW (Braithwaite *et al.* 1983; Cork 1992). A shift of even 20% of that seen in seedlings would cause a large proportion of the communities presently supporting greater gliders to shift to the unfavourable side of the postulated toxicity threshold (figure from Cork and Foley 1997)

also limiting, as well as when plants are growing in mixed communities. Second, studies elsewhere have shown that the more extensive free-air CO₂ enrichment of field-grown plants leads to less dramatic changes in foliar nitrogen. Finally, complicating the matter is how the predicted increases in concentrations of other atmospheric gases, especially ozone, will influence foliar chemical concentrations. In several studies of the tree, quaking aspen, in the USA, Lindroth and colleagues (Kopper and Lindroth 2003) showed that O₃ had the opposite effect to CO₂ on foliar nitrogen and phenolic-based secondary metabolites. Although climate change may alter the chemical composition of foliage, there is little evidence to support the views of Kanowski (2001) that marsupials are in danger of being poisoned by their food as atmospheric CO₂ rises. Instead we need more studies of plant responses and the effects they may have on animals of different trophic levels.

In the long term, the more pertinent issue of climate change is not so much how it influences leaf chemistry but how it affects the distribution of eucalypt species. Most species (68%) have ranges covering less than 1% of Australia, 97% cover less than 10% while only two species cover more than 40% (Hughes *et al.* 1996a). More importantly, 53% of species have ranges spanning less than 3°C of mean annual temperature and 25% have a range spanning less than 1°C (Hughes *et al.* 1996b). The projected rise in temperatures would completely displace these species from the temperature profiles they now inhabit. Similarly, global warming is likely to exacerbate any differences that may exist in the temperature tolerances of monocalypts and of symphyomyrts (Anekonda *et al.* 1999). Thus, the effect of climate change, especially increasing temperature, fluctuating rainfall and fire, on local habitats may determine the future distribution of eucalypt species and the animals that rely on them. Equally pertinent are the words of Specht (1996) and Specht and Specht (1995), who used community-physiology principles to predict the effect of a 2 - 4°C rise in temperature and associated rainfall patterns on the structure of eucalypt communities in southern Australia. They predict that a tall open-forest would change to an open-forest; an open-forest to a woodland; a woodland to an open scrub. They conclude: "the flexibility of today's eucalypt communities during climatic change will be severely tested."

All of these views disregard phenotypic flexibility - the set of ontogenetic trajectories that a genotype can produce when it is exposed to different environmental conditions (Schlichting and Pigliucci 1995). We know little about the set of phenotypes that eucalypts may produce under the environmental conditions that can be expected in the next 30 - 100 years. In other genera, both population size and population identity (family groups within populations) can affect growth and survival across environmental stress gradients (Paschke *et al.* 2003). Thus, genetic variation in the reaction norm for growth traits and in the patterns of biomass allocation is critical to phenotypic evolution in heterogeneous environments.

The marsupial folivores and eucalypts have existed and evolved together over millions of years. During this period, ecosystems have adapted to and survived periods of climate change, extinctions and introductions of predators, and changes in hunting pressure and fire intensity brought about by Aboriginal people. If

we now want to ensure that populations of marsupial folivores continue to remain secure, we need a firm understanding of their ecology and how our activities affect it. Understanding the nutritional basis of why and how marsupial folivores are found where they are is essential to this aim.

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Appendix I. Eucalypt taxa mentioned in this chapter. Taxonomy is based upon Hill and Johnson (1991a; 1991b; 1995); distribution refers to natural distribution only, by state (QLD = Queensland, NSW = New South Wales, VIC = Victoria, SA = South Australia, TAS = Tasmania).

Genus	Subgenus	species	Common names	Distribution
<i>Corymbia</i>			Bloodwoods, spotted gums, ghost gums	
		<i>citriodora</i>	lemon-scented gum	QLD
<i>Eucalyptus</i>				
	<i>Monocalyptus</i>		Ashes, peppermints, stringybarks, white mahoganies	
		<i>acmenoides</i>	white mahogany	QLD, NSW
		<i>agglomerata</i>	blue-leaved stringybark	NSW, VIC
		<i>andrewsii</i>	New England blackbutt	QLD, NSW
		<i>consideniana</i>	yertchuk	NSW, VIC
		<i>dives</i>	broad-leaved peppermint	NSW, VIC
		<i>elata</i>	river peppermint	NSW, VIC
		<i>fastigata</i>	brown barrel	NSW, VIC
		<i>fraxinoides</i>	white mountain ash	NSW
		<i>globoidea</i>	white stringybark	NSW, VIC
		<i>haemastoma</i>	broad-leaved scribbly gum	NSW
		<i>obliqua</i>	messmate	QLD, NSW, VIC, SA, TAS
		<i>radiata</i>	narrow-leaved peppermint	NSW, VIC, TAS
	<i>Nothocalyptus</i>		tallowwood	
		<i>microcorys</i>	tallowwood	QLD, NSW
	<i>Symphyomyrtus</i>		Gums, boxes, ironbarks	
		<i>baueriana</i>	blue box	NSW, VIC
		<i>cladocalyx</i>	sugar gum	SA
		<i>cypellocarpa</i>	monkey or mountain grey gum	NSW, VIC
		<i>dalrympleana</i>	mountain gum	NSW, VIC, TAS
		<i>globulus</i>	blue gum	NSW, VIC, TAS, SA
		<i>globulus</i> <i>ssp. maidenii</i>	Maiden's gum	NSW, VIC
		<i>longifolia</i>	woollybutt	NSW, VIC
		<i>meliiodora</i>	yellow box	QLD, NSW, VIC
		<i>nitens</i>	shining gum	NSW, VIC
		<i>nobilis</i>	forest ribbon gum	QLD, NSW
		<i>ovata</i>	swamp gum	NSW, VIC, SA, TAS
		<i>polyanthemos</i>	red box	NSW, VIC
		<i>punctata</i>	grey gum	QLD, NSW
		<i>sideroxylon</i>	red ironbark, mugga	QLD, NSW, VIC
		<i>tereticornis</i>	forest red gum	QLD, NSW, VIC
		<i>viminalis</i>	manna, ribbon or white gum	NSW, VIC, SA, TAS
		<i>viminalis</i> <i>ssp. pryoriana</i>	Gippsland manna gum	VIC

APPENDIX 2



The four marsupial folivores of *Eucalyptus*, clockwise from top left: koala (Photo: Ben Moore), common brushtail possum, greater glider and common ringtail possum.

The common brushtail possum spends more time foraging on the ground than the other marsupial folivores, but eucalypt foliage often accounts for the majority of its diet. This brushtail is feeding on red ironbark *Eucalyptus sideroxylon*. Photo: Karen Marsh

The common ringtail possum feeds from eucalypts and myrtaceous understorey species. This captive ringtail is feeding on scribbly gum *Eucalyptus rossii*. Photo: Karen Marsh

The greater glider's diet consists almost exclusively of eucalypt leaves, in particular young foliage. The extremely patchy distribution of this species is closely linked to the nutrient status of eucalypt forests. Photo: Bill Foley

APPENDIX 2



A major challenge for the koala translocation scheme in Victoria is to identify areas of suitable koala habitat. Koalas are sometimes released into areas without pre-existing koala populations. With a better understanding of the koala's nutritional requirements, we should be able to assess whether koalas are absent because the forest is nutritionally or chemically inadequate, or whether historical factors explain the absence of koalas. In this photo, a male koala from French Island is released in Mount Disappointment State Forest. Photo: Ben Moore



Intense bushfires kill many folivores directly and in the short term, they destroy the food resource for remaining animals. Subsequent epicormic regrowth can be vigorous and highly nutritious. However, the concentration of plant toxins in this foliage has not been studied and may limit its palatability. Photo: Ben Moore

APPENDIX 2



Our understanding of folivore diets is largely based on feeding experiments with captive animals, because it can be very difficult to observe nocturnal, arboreal species feeding in the wild. Marsupial folivores may visit trees for many reasons other than feeding, such as maintaining social contact, sampling foliage, resting and seeking shelter. Thus, mere observations of tree visits by free-ranging animals can provide a misleading picture of their feeding preferences. On Phillip Island, Victoria, we are using radio collars fitted with microphones to obtain a detailed picture of how much koalas eat when they visit different individual trees. Here, Ben Moore releases a newly collared koala. Photo: Ben Moore



Defoliation of *Eucalyptus viminalis pryoriana* by koalas at Sandy Point, Victoria. Such intense herbivory can only occur when population growth and feeding is not limited by the nutritional quality of foliage. In contrast to the trees pictured, *Eucalyptus radiata* at Sandy Point remains relatively untouched by koalas. It has been suggested that the development of a dense understorey layer, like the bracken in this photograph, causes tighter nutrient cycling and leads to more nutritious eucalypt foliage. Photo: Ben Moore