

Managing habitat for mycophagous (fungus-feeding) mammals: a burning issue?

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ABSTRACT

In the past two decades the ecological relationships among mycophagous (fungus-feeding) mammals and their fungal food resources have been variously investigated. An unresolved issue stemming from this research is the importance of fire in creating and enhancing fungal supply for animals such as potoroos, bettongs and bandicoots. Some authors have suggested fire is a major positive influence, because it stimulates fruit-body production by fungi and is therefore necessary for mycophagous mammals to survive. However, careful review of relevant literature identifies no clear pattern in effects of fire on the wide range of hypogeous fungi eaten by mammals. Evidence of a 'co-evolutionary relationship', as some authors have implied, is also ambiguous. We are concerned that some land management agencies, which use prescribed fire for hazard reduction or silvicultural purposes, selectively use speculative data about fire effects on hypogeous fungi to further justify the fire regimes they ordinarily apply. A series of rigorous studies is necessary to better understand the effects of fire on the fruiting of hypogeous fungi and how that influences populations of mycophagous mammals.

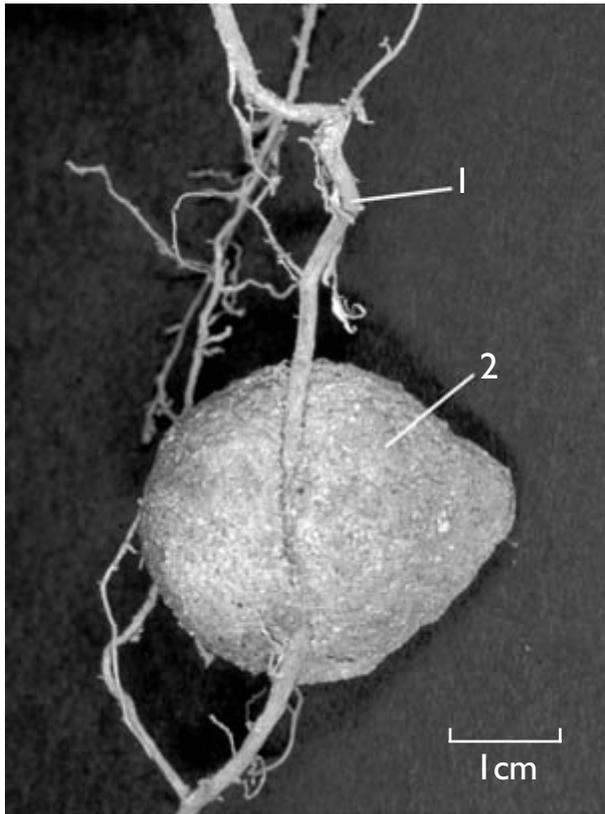
Key words: fire, Mesophelliaceae, hypogeous fungi, habitat, marsupials, mycorrhizae.

Introduction

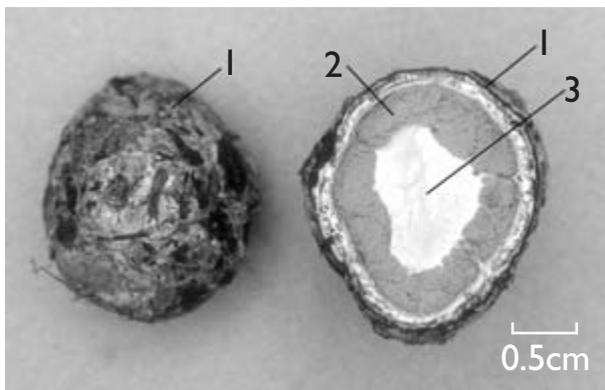
The varied interactions among mycophagous (fungus-feeding) ground-dwelling mammals, hypogeous (underground-fruiting) mycorrhizal fungi and woody plants have been the focus of considerable research in Australia (eg. Lamont *et al.* 1985; Malajczuk *et al.* 1987; Taylor 1991, 1992, 1993a,b; Claridge *et al.* 1992, 1993a,b,c; Claridge and Cork 1994; Johnson 1994a,b,c,d; Lamont 1995; Vernes 2000; Vernes and Haydon 2001; Vernes and Pope 2001; Vernes *et al.* 2001). Lamont (1995) argued that each contributor to this three-way association benefits from the others as follows: (i) the animal benefits nutritionally by consuming the fruit-bodies of hypogeous fungi, (ii) the fungus benefits from its host plant by receiving photosynthates, (iii) the plant benefits by receiving nutrients and water from the fungus, and (iv) the fungus benefits from the animal, which acts as a dispersal agent of the fungal spores it has consumed but cannot digest (Maser *et al.* 1978).

Bougher and Lebel (2001) estimated that well over a thousand species of hypogeous fungi likely occur in Australia. Claridge *et al.* (2000a,b) developed models for the habitat requirements of several such species, specifically from the south-eastern mainland part of the continent. They demonstrated that different taxa have strongly differing habitat requirements. Trappe, Cork and Claridge (unpublished data) have found that the xeric box-ironbark woodlands of eastern Australia have mostly different species than the more mesic sites sampled by Claridge *et al.* (2000a,b). Individual species in this rich array, occurring over a great diversity of habitats, can therefore be expected to respond in a variety of ways to any particular disturbance to their habitat.

Despite the recently expanded understanding of the interrelationships among mycophagous mammals, hypogeous mycorrhizal fungi and plants (Claridge 2002; Luoma *et al.* 2003), the effects of disturbances, such as fire and logging, on this triangular trophic association remain poorly understood (Claridge and May 1994; Lamont 1995). Some authors have suggested that fire benefits mycophagous mammals by stimulating production of mature hypogeous fungal fruit-bodies between three and seven days post-fire (Taylor 1991; Johnson 1995). This hypothesis was based initially on the observation that the foraging activity by these animals for hypogeous fungi in a limited number of habitats may increase substantially very soon after a forest is burnt (Christensen 1980; Taylor 1991; Vernes 2000). In all cases, the fungi in question were members of the family Mesophelliaceae (Trappe *et al.* 1992, 1996a,b), particularly the genus *Mesophellia*, which is endemic to eucalypt-dominated forests and woodlands of Australia (Dell *et al.* 1990, Trappe *et al.* 1996b) and specific to certain kinds of habitats (Claridge *et al.* 2000b). *Mesophellia* fruit-bodies have a hard, brittle outer skin or peridium, a fleshy inner peridium in which mycorrhizae of associated host trees develop, and a central core of firm to leathery tissue which is the main nutritional component sought by the animal mycophagist (Claridge and Cork 1994 – see Figure 1). The fruit-bodies may form just below the soil-litter interface to as deep as 40 cm (Dell *et al.* 1990; Claridge 1992). They become increasingly aromatic as they mature, and the odours appear to attract mycophagous mammals (Donaldson and Stoddart 1994).



1. Eucalypt rootlet. 2. Fruit-body of *Mesophellia glauca*.



1. Peridium. 2. Spore mass. 3. Columella or sterile core

Figure 1. Fruit-bodies of *Mesophellia* from an unburnt site, surface and cross-sectional views. These specimens had a pleasant, nutty odour.

The effects of fire on habitat for mycophagous mammals are complex, so no single component, such as production of hypogeous fungi, could sensibly be separated from the others, such as shrub cover (e.g. Claridge and Barry 2000; Monamy and Fox 2000). The better each component is understood, the better can the pieces be integrated into a holistic approach to the use of fire for specific management purposes. It is timely to look anew at effects of fire on availability of hypogeous fungi, especially the genus *Mesophellia*, as a food resource for mammals. As a test of the hypothesis that fire enhances fruiting of hypogeous fungi, we present new data on the occurrence and fruiting patterns of the genus *Mesophellia* and effects

of the 2003 fires in the Australian Alps on fruiting of hypogeous fungi. We also review literature dealing with morphogenesis and phenology of fungi, as well as the effects of fire on fruit-body production of hypogeous fungi specifically. Conclusions from this review are couched in terms of implications for management of habitat for mycophagous mammals.

Studies on the distribution, fruiting patterns and habitat requirements of the genus *Mesophellia* in south-eastern Australia

An extensive study of the distribution, fruiting patterns and habitat requirements of *Mesophellia* was carried out by Claridge *et al.* (2000a, b). In these studies, 136 plots, each 50 x 20 m, were established in East Gippsland, Victoria and the adjacent south-eastern corner of New South Wales. Sites were selected across major environmental gradients to allow the sampling of fungi in a diversity of forest habitats. At each site, a range of habitat characteristics was recorded, including forest composition, climatic parameters, substrate geology, topography, disturbance history including time since last fire, leaf litter depth, and abundance of coarse woody debris, stumps and stags. Hypogeous fungi were sampled by raking with 4-tined garden cultivators as deep as 15 cm for 100 person minutes. This time constraint method had been determined as providing a high probability that all taxa that were fruiting would be detected and that about 20% of the plot surface would be disturbed. The time-constraint approach was adopted to minimise the large proportion of plots with zero fruit-bodies typical of small plots, a result of the notably patchy occurrence of ectomycorrhizal fungi.

All hypogeous fruit-bodies encountered were collected and, when a *Mesophellia* fruit-body was unearthed, its colony was mined both horizontally and vertically to collect its other fruit-bodies. At the end of each day, the specimens were sorted and counted by species, their fresh characteristics recorded and representative specimens photographed. They were then dried overnight on a portable dehydrator and the specimens bagged and subsequently identified by use of published and unpublished keys and descriptions.

All plots were sampled, in this way, five times: autumn and spring 1996 and autumn 1999, 2001 and 2003. The 1996 spring sampling yielded relatively few fruit-bodies, so only autumn sampling was conducted thereafter. Across all sample periods, 53 of the 136 plots yielded *Mesophellia* fruit-bodies (Table 1). On 21 (40%) of these, *Mesophellia* fruit-bodies were found at only 1 of the 5 sampling times; on 10 (19%) at 2 of the 5 times; on 14 (26%), at 3 of the 5 times; on 5 (9%), at 4 of the 5 times; and on only 3 (6%) at all 5 sampling times. Numbers of plots producing *Mesophellia* fruit-bodies at individual sampling times ranged from 12 at autumn 1996 (23% of the 53 overall producing plots) to 34 in spring 1996 (64% of the total producing plots) (Table 1). Numbers of *Mesophellia* fruit-bodies in individual plots at individual

sampling times ranged from 1-24 in spring 1996 to a high of 60 in autumn 2003. With all years combined, the numbers of fruit-bodies found in individual plots ranged from 1-115. Relatively high fruit-body production (10 or more) occurred at only 19 (36%) of the 53 plots, all sampling times combined; at any given sampling time, the number of plots with 10 or more fruit-bodies ranged from 2-9 out of the 53. Only 5 plots produced 10 or more fruit-bodies at two or more sampling times. Very high fruit-body production (20 or more) occurred on only 13 plots; of these only two had 20+ fruit-bodies at 2 of the 5 sampling times, and 11 at only one sampling time.

This study, designed to detect taxa present in various habitats, showed that over five sampling times, *Mesophellia* spp. were encountered at about 40% of all sites sampled. The explanatory model for *Mesophellia* spp. indicated that the probability of occurrence of fruit-bodies increased with increasing annual mean moisture index, and was lowest at sites that were long unburnt (Claridge *et al.* 2000a). Although the study was not designed to estimate total fruit-body productivity on plots, some patterns were evident. Fruit-body production on sites containing *Mesophellia* varied strikingly between sites, and within individual sites between sampling times. From these data we concluded that fruit-body production on those sites that contained *Mesophellia* varied markedly between years and seasons.

Evidence on response of *Mesophellia* to fire

Studies on direct effects of fire on hypogeous fungi initially dealt only with fruit-body production until molecular methods enabled the study to be made of the survival of fungal mycelium in the soil under conditions changed by fire, or succession of fungal species in the years following fire. Gardes *et al.* (1991) and Gardes and

Bruns (1996) confirmed that the production of fruit-bodies of mycorrhizal fungi (i.e. those that form symbiotic associations with feeder rootlets of many tree genera such as *Eucalyptus*) reflects only a fraction of the total number of species at a site. In terms of mammal mycophagy, however, actual production of hypogeous fruit-bodies is the key issue.

The deep colonies of *Mesophellia* species and hard outer peridium of their fruit-bodies enable the mycelium, and any fruit-bodies present at time of burning, to survive fire better than fungi with more shallow growth and fruiting habits (Claridge 1992). Most species produce soft, fleshy fruit-bodies near or only a few centimetres below the interface of the soil organic and mineral layers (Claridge *et al.* 2000a,b), the zone most likely to reach lethal temperatures during fire (Auld and Bradstock 1996; Bradstock and Auld 1995; Bradstock *et al.* 1992). A paired plot comparison of the production of hypogeous fungi in two moderate-intensity prescribed burns set to reduce fuel loads versus adjacent non-burnt forest by Trappe, Claridge and Cork (unpublished) in the Australian Capital Territory showed that: (i) one month after the burn, at the peak time of autumn sporocarp production, the burnt plots produced none, or very few fruit-bodies, whereas production on unburnt plots was high, and (ii) one year later, the burnt plots had recovered to equal the unburnt plots in both species diversity and the number of fruit-bodies produced, except for one species, *Dermocybe globuliformis*. Members of the Mesophelliaceae were infrequent on sites of either treatment, and no burning effect was evident for them. *Dermocybe globuliformis* is instructive because it produces easily recognised, bright yellow aggregates of mycelium, typically in the lower organic horizons or only one centimetre or so deep in the mineral soil. One month after the burn, the moist, brightly coloured mycelium in unburnt plots produced abundant fruit-bodies, whereas

Table 1. Occurrence and abundance of *Mesophellia* fruit-bodies in five samplings for hypogeous fungi on 136 (50 × 20 m) plots in south-eastern mainland Australia (Claridge *et al.* 2000a,b). *Mesophellia*-containing plots are those that produced fruit-bodies in at least one sampling time.

Attribute of Plot	Sampling Year (a = autumn; s = spring)					All
	1996a	1996s	1999a	2001a	2003a	
No. of sites producing <i>Mesophellia</i> fruit-bodies out of a total of 136 sites	12	34	19	25	28	53
% of sites producing <i>Mesophellia</i> fruit-bodies out of a total of 136 sites	8	25	14	18	21	39
% of sites producing <i>Mesophellia</i> fruit-bodies out of 53 sites containing colonies of the genus after all years combined	23	64	35	47	53	100
No. of <i>Mesophellia</i> fruit-bodies found from all sample sites	80	179	145	163	276	843
Mean no. of <i>Mesophellia</i> fruit-bodies per producing site	6.7	5.3	7.6	6.5	9.9	15.9
Range of number of <i>Mesophellia</i> fruit-bodies at individual producing sites	1-25	1-24	1-36	1-32	1-60	1-115
Number of sites producing 10 or more <i>Mesophellia</i> fruit-bodies	2	7	4	6	9	19
Number of sites producing 20 or more <i>Mesophellia</i> fruit-bodies	1	1	2	1	4	6

the mycelium in the burnt plots was dull, faded and dry. One year after fire, numerous brightly-coloured mycelium aggregates of *D. globuliformis* appeared in the burnt plots, but only few fruit-bodies formed as opposed to a huge production in the non-burnt plots.

The data from our long-term monitoring of hypogeous fungi in south-eastern mainland Australia (Claridge *et al.* 2000a,b) further show these differences. The fifth sampling was in autumn 2003, after the wildfires in the Australian Alps burned 17 of the 53 plots known to contain colonies of *Mesophellia* spp. Table 2 shows that the mean number of species found on the plots in the four samplings before 2003 varied from year to year, but overall they were roughly similar. After the fire, however, the mean number of species in the 17 burned plots was only 1.8, compared to 6.7 in the 36 unburnt plots. With few exceptions, the species fruiting in the burnt plots were *Mesophellia* spp. When *Mesophellia* spp were subtracted from the total numbers of species, the means for unburnt plots remained close. On the burnt plots, however, the mean when *Mesophellia* spp. are excluded (0.9) is only half that when they are included. In other words, *Mesophellia* fruiting was equivalent to all other species combined on the burnt plots. Animals foraging on unburnt sites would encounter diverse species. Those foraging on burnt sites would find mostly *Mesophellia* spp.

The major conclusions from our long-term data are: (i) different species respond differently to fire in both mycelium survival and sporocarp production, and (ii) species and growth habit influence rate of recovery from fire. One can thus predict that deep-fruiting fungi with hard outer peridia, such as *Mesophellia* spp, will survive fire better than shallow-fruiting species with fleshy fruit-bodies. Moreover, the Mesophelliaceae have long-lived fruit-bodies that can be found throughout the year (Claridge *et al.* 1993b), whereas fruiting of species with short-lived, fleshy fruit-bodies is more seasonal and responsive to available moisture and typically occurs only days or weeks after the soil has been well wetted (Johnson 1994a). Because both prescribed fire and wildfires normally occur when soil moisture is low, available fruit-bodies occurring soon after fire are likely to be those that persist deep in the soil, such as the Mesophelliaceae, rather than fleshy species.

The original hypothesis that fire stimulated production of fruit-bodies by *Mesophellia* came from anecdotal field observations of the foraging activity of mycophagous mammals in recently burnt habitats. In Western Australia, Christensen (1980) noted that foraging by Brush-tailed Bettongs *Bettongia penicillata* for *Mesophellia* fruit-bodies increased dramatically in burnt areas only a few days after the flames had gone out. Similarly, in northern Tasmania, Taylor (1991) observed that the foraging activity of Tasmanian Bettongs *Bettongia gaimardii* in recently burnt woodland was 10-fold greater than in unburnt areas, and that this increased activity began a few days after fire. Most forage-diggings in the burnt plots had the remains of fungal fruit-bodies, which were all members of the Mesophelliaceae.

What could account for this phenomenon? There are at least four alternative hypotheses. Firstly, fire may remove ground cover which normally impedes foraging for mycophagous mammals, thereby improving access to the soil and hence food resources. Secondly, animals may dig more often for fungi in recently burnt habitats because other foods have become unavailable. Thirdly, fire may actually cause the Mesophelliaceae to fruit. And fourthly, heating of fruit-bodies of Mesophelliaceae may change their odour to make them more detectable.

To help determine the nature of the post-fire foraging response by mycophagous mammals, Johnson (1995) set up experimental burns in a Tasmanian woodland dominated by *Eucalyptus tenuiramus*, which was the preferred habitat of a local population of Tasmanian Bettongs. A series of matched sites was established, some subject to deliberately applied (prescribed) fire, the others remaining as unburnt sites. The first of two related experiments was on a small scale, in which the foraging activity of bettongs and the relative abundance of fruit-bodies was estimated. In this initial trial, the fruit-bodies were sampled from immediately around trees that either burnt at high or low intensity or were not burnt at all. In the second experiment, conducted at a larger scale, the foraging activity, relative abundance of fruit-bodies, and the local population of bettongs were monitored. This trial differed from the first in as much as fruit-bodies were sampled from within enclosures around randomly marked trees before the application of fire. The enclosures prevented harvest of fruiting bodies by the bettongs. In both experiments, the relative abundance of fungal fruit-bodies was estimated across all sites two months before fire, then one week, and two, four, six and 10 months post-fire.

Table 2. Mean number of species occurring in five samplings for hypogeous fungi on 53 (50 × 20 m) *Mesophellia*-containing plots in south-eastern mainland Australia (Claridge *et al.* 2000a,b); in the fifth sampling year, 17 plots were burnt by wildfire, 36 were unburnt. *Mesophellia*-containing plots are those that produced fruit-bodies in at least one sampling time.

Attribute of Plot	Sampling Year (a = autumn; s =spring)				
	1996a	1996s	1999a	2001a	2003a
Mean no. of species in 17 burnt sites known to contain <i>Mesophellia</i> spp.	7.9	3.4	7.9	5.2	1.8
Mean no. of species in 36 unburnt sites known to contain <i>Mesophellia</i> spp.	7.5	3.1	8.0	8.6	6.7
Mean no. species in 17 burnt sites, excluding <i>Mesophellia</i> spp.	7.2	2.9	7.5	4.9	0.9
Mean no. species in 36 unburnt sites, excluding <i>Mesophellia</i> spp.	6.1	2.4	7.6	8.0	6.4

In the first set of small-scale fires, the density of forage-diggings of bettongs increased by three-fold within one month post-fire, then within four months it had returned to pre-fire levels and matched forage-digging densities on unburnt sites. A similar result was recorded during the second experiment, with the density of forage-diggings increasing by eight-fold. The relative abundance of fungal fruit-bodies changed, but these changes differed in relation to the intensity of fire. In the first set of small-scale burns, the relative abundance of fruit-bodies from plots in control sites did not differ from plots around trees burnt at low intensity. However, in plots around trees burnt at high intensity, the density of fungal fruit-bodies was much greater than in plots burnt at low intensity or unburnt plots. This response occurred in sampling undertaken only immediately post-fire, and within two months, the densities of fruit-bodies equalled those around trees burnt at lower intensity and trees in unburnt sites. However, six months post-fire, fruit-body densities were significantly higher around trees on unburnt sites. The overall result was that long-term productivity of fungal fruit-bodies did not differ significantly across all sites, whether burnt or not. Changes in productivity immediately post-fire were largely attributed to species within the Mesophelliaceae, particularly *Mesophellia*. In the second experiment, in which fruit-bodies were collected from within the enclosures that prevented bettong foraging, fruit-bodies did not significantly increase around trees on burnt plots. Instead, fungal productivity on the burnt site remained stable. This contrasted with the unburnt control site, where fungal productivity decreased after one month post-fire, but later recovered and surpassed that on the burnt site at 7 and 10 months post-fire. Despite the fact that fungal productivity did not increase on the burnt site in this second trial, the foraging response by the animals was the same - increasing prolifically immediately post-fire. Such a result is perplexing from the point of view of reaffirming the notion that fire stimulates hypogeous fungi to fruit.

Did fire trigger fungal fruiting in the first of the two experimental burns of Johnson (1995)? The results of the two separate burns indicate that fungal response to fire is complicated and perhaps unpredictable. Marked changes in fungal abundance post-fire were recorded only once. What might have triggered that peak is unknown. Johnson (1995) hypothesised that the causal factors might include one or more of the following: (i) the soil being heated and dried, (ii) (unknown) chemical effects on plant roots and fungi, (iii) the rapid release of nutrients held in litter, (iv) actual damage to the fungi or above-ground plant parts, resulting in some (unknown) phenological response, or (v) some physiological change in the plants. Another possibility is that the peak simply reflects the non-random, clumped distribution of hypogeous fungi (Fogel 1976, Hunt and Trappe 1987, Gomez *et al.* 2003). As in the previous anecdotal observations, in Johnson's study the changes occurred exclusively in the Mesophelliaceae. Whatever the cause, the increase in foraging activity by bettongs immediately post-fire is rapid.

Similar experimental burning in the habitat of the Northern Bettong *Bettongia tropica* at Davies Creek in north-eastern Queensland (Vernes 2000; Vernes *et al.* 2001) largely corroborates the patterns observed by Johnson (1995) in Tasmania. However, a clear understanding about the stimulating influence of fire on fungal fruiting is hampered because sample plots for fungal fruit-bodies were placed on or immediately adjacent to sites where Northern Bettongs had dug. Therefore, the patterns observed may reflect the foraging preferences of animals rather than a response by the fungal population *per se*. Notwithstanding, the biomass of fungal fruit-bodies under forage-diggings was higher on burnt sites than on unburnt sites after fire, but it soon returned to pre-fire levels. In keeping with all previous studies, members of the Mesophelliaceae were the only taxa found more often after fire and again only for a short time.

By using spool and line tracking (a technique of attaching a spool of thread to animals and following the line to determine each movement an animal makes), Vernes and Haydon (2001) established that significantly more Northern Bettongs chose to forage in burnt than in unburnt habitat shortly after fire. The remains of fungi left by animals were found more frequently at diggings in burnt sites compared to unburnt sites. Whether this pattern truly indicated increased fruiting of fungi is uncertain, because animals in burnt sites mainly fed on Mesophelliaceae while animals in unburnt sites mainly fed on other fungi. Remains of Mesophelliaceae are more likely to be left at forage-diggings by virtue of the manner in which fruit-bodies are eaten: the sterile outer shell is typically cracked open and discarded, whereas the fruit-bodies of most other fungi are ingested whole (Claridge and May 1994), so no traces can later be observed.

Morphogenesis of hypogeous fungal fruit-bodies

A review of fungal fruit-body morphogenesis helps our understanding of the timing of development of *Mesophellia* in relation to time since fire. Fruit-bodies of both epigeous and hypogeous fungi are initiated as primordia, in which the major structures are differentiated in miniature (Moore 1998; Stamets 2000). Primordium formation may be fast, but at a minimum requires several days, and most fungi require weeks or months depending on environmental conditions. The initiation of primordia is triggered by a shift in environmental variables, primarily moisture, air exchange, temperature and light (Stamets 2000). Once fully formed and given the appropriate physiological signal by these variables, the primordium expands and produces its spore-bearing structures, in this case basidia or asci. Upon completion of that expansion and the full development of the basidia or asci, the fruit-body forms sexual spores.

Expansion of the primordium to the mature, spore-producing fruit-body may take as little as 12 hours to as much as several months, depending on the individual species. In general, species that expand rapidly do so by the rapid water uptake that inflates the cells to produce a fragile, ephemeral sporocarp (Moore 1998). For example, the phalloid species

Dictyophora indusiata emerges from its fully developed 'egg' stage below-ground, expands, exposes the pre-formed spores to insects, and collapses in less than 24 hours (J.M. Trappe, unpublished data). This rapid expansion not only entails inflation of cells but also a lattice structure of the stem that further speeds expansion as the cells forming the lattice inflate from imbibed water.

Phenological data on sporocarp formation have been developed mostly for species grown under cultivation. Stamets (2000) provided the timing of primordium formation and sporocarp formation for 31 species of saprobic fungi (those that grow on dead organic matter), cultivated under ideal, controlled conditions. Primordium formation requires three to five days and subsequent expansion of fruit-bodies another three to five days for some fleshy and fragile species to as much as 60 to 90 days for certain leathery or woody species. Fruiting of these fungi in uncontrolled natural conditions can take much longer because the environmental variables are rarely ideal.

In studies of the fruiting phenology of a wide array of fungi in nature, Weber (2002) found that a few fragile, fleshy, saprobic mushroom species formed fruit-bodies that matured and senesced within two weeks, but most other species required longer. Some fleshy Ascomycetes did not produce spores for one to two months after the fruit-bodies appeared. Weber noted that "... the majority of short-lived fruiting bodies are relatively fragile and lack woody tissue. In contrast, fruiting bodies that produce spores for weeks or even months tend to be tough, fibrous or gelatinous."

Little has been reported on the phenology of ectomycorrhizal fungi. Primordium formation occurs in the soil and thus is normally difficult to observe. *Russula* species have tissues composed largely of thin-walled, inflatable cells termed sphaerocysts. These species usually take a week or more to expand beyond the primordial stage even under favourable conditions (J.M. Trappe and A.W. Claridge, personal observations). Other groups of fungi expand their fruit-bodies from the primordium by a combination of cell inflation and the growth of new cells (Moore 1998). *Laccaria bicolor* represents this strategy, with a considerable proportion of its expansion resulting from growth of new cells. It takes two or more weeks to expand fully to spore-bearing stages under glasshouse (ideal) conditions (J.M. Trappe, personal observations). *Scleroderma laeve*, a puffball with a thick, leathery peridium, takes more than four weeks to mature from the primordial stage under favourable moisture conditions, and even longer if warm, dry periods occur during its development.

Hypogeous fungi normally expand entirely below ground; consequently data on the timing of their primordial development and expansion are difficult to obtain. As most hypogeous fungi (fleshy species that fruit below ground) are related to mushroom species in the groups that expand by a combination of cell expansion and cell growth, we can infer for the hypogeous species that sporocarp expansion and maturation typically require two or more weeks. This inference is supported by direct observations on the phenology of some fleshy hypogeous species. R. Mowrey (Wildlife Biology Consultant, personal communication, March 2003) found *Hysterangium coriaceum* fruiting

under a moss carpet in a spruce stand in Alaska. The moss could be rolled back like a carpet to reveal the underlying fruit-bodies without disturbing them. Repeated visits to the site showed that fruit-bodies typically required at least two weeks to develop from the primordial stage to mature size (1-2 cm in diameter) when the weather was favourable (i.e. cool and moist), but up to four or more weeks were needed if temperature and moisture were sub-optimal. R. Young (Mycorrhizal Applications Inc., personal communication, March 2003) observed a similar timing for the fleshy *Rhizopogon occidentalis* in a pine forest in southern Oregon, where fruit-bodies formed on the soil surface under deep leaf litter that could be removed and replaced without harming the fungal colonies. N. Weber (Oregon State University, Department of Forest Science, personal communication, March 2003) observed that *Hymenogaster* and *Rhizopogon* spp required two to four weeks to expand to maturity, depending on the weather.

Johnson (1994a) related maturation of fruit-bodies of hypogeous fungi to lag time since rainfall in a Tasmanian eucalypt woodland. Different groups of taxa responded to rainfall in different and sometimes contrasting ways. In general, fleshy species fruited when the soil was moist, whereas occurrence of *Mesophellia* spp. showed no relationship with rainfall and either fruited during dry periods or persisted into dry periods.

The suggestion that fruit-bodies of species of the Mesophelliaceae expand and mature within a few days after fire would require a developmental acceleration otherwise known only for fragile, saprobic fungi such as *Dictyophora indusiata*, which is composed mostly of cells that rapidly inflate through water uptake and have a lattice structure that speeds sporocarp expansion. The Mesophelliaceae is a unique family; its phenology cannot be inferred from a relationship to observed mushrooms. Studies by Dell *et al.* (1990) and Trappe *et al.* (1992, 1996a,b) show an anatomy typical of fungi that expand mostly through cell growth. Most of the fruit-body tissues are composed of narrow cells with strongly gelatinised walls and few or no inflated cells. The outer peridium is leathery to brittle and in some species is darkly pigmented, characters typical of slowly developing fungi such as the woody pore fungi on trees that require 7-60 days to develop primordia and 30-90 days to expand and mature (Stamets 2000). Perhaps most strikingly, by maturity the inner peridium of species of *Mesophellia* is permeated with mycorrhizal feeder rootlets of associated host trees. Dell *et al.* (1990) found that mature fruit-bodies of *Mesophellia trabalis* contained an average of five metres of such rootlets. These cannot develop within a few days or a week. Dell *et al.* (1990) believed that "the fruit-bodies probably take several months to mature before all root connections with the host are severed ..."

Taylor (1992) challenged this idea as "... an opinion with no data to back up the claim" and suggested that "fire could well induce physiological changes in the plant host and/or the fungus, or changes to their environment, which could dramatically alter sporocarp growth rates." Fire and its aftermath could potentially shift the environmental variables that control primordium formation and fruit-body expansion and maturation. However, no known mechanism exists to

produce the growth of fruit-bodies with the mesophellioid anatomy and five metres of incorporated rootlets in less than several weeks under even the most ideal conditions. Johnson's (1994) data on abundance of hypogeous fungal fruiting as correlated with time lag since rain suggested to him that *Mesophellia* spp. required two to three weeks for fruit-body maturation, less than that suggested by Dell *et al.* (1990) but more than the few days suggested by Taylor (1992). Taylor's view was not based on direct phenological observations and is improbable for fungi with the anatomy of the Mesophelliaceae.

An alternative hypothesis

If fire does not directly stimulate the fruiting of *Mesophellia*, what else might explain the foraging response of mycophagous mammals in the first few days after fire? We propose that the answer lies not in the notion that these fungi become more abundant immediately post-fire, but rather that they are already present but become more attractive to the animals. When we sampled the plots burnt by the fires of 2003 in our long-term monitoring of hypogeous fungi (Claridge *et al.* 2000a,b) we found that specimens near the soil surface were frequently charred and had a strong odour of smoky rotting

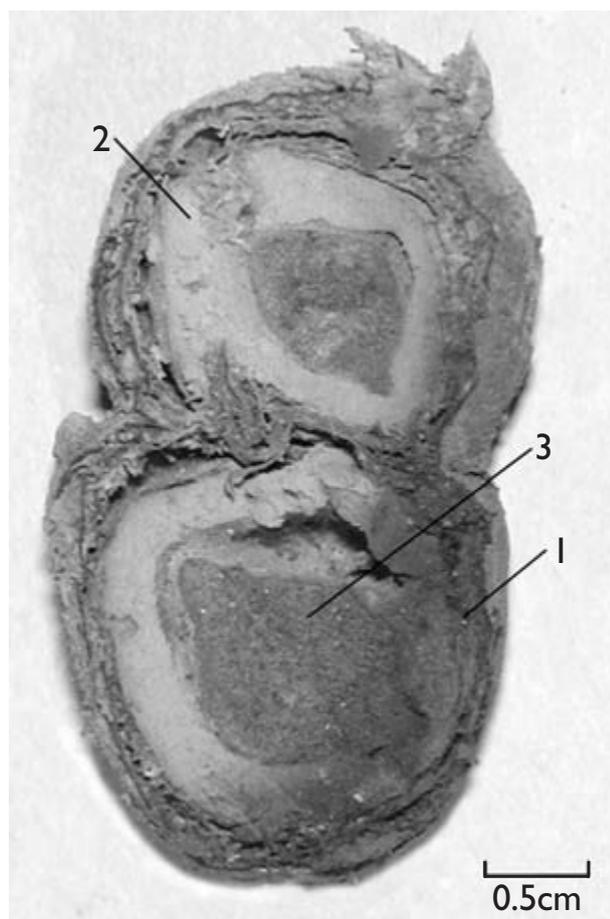
onions (Figure 2). Deeper specimens showed neither of these characteristics. Millington *et al.* (1997) demonstrated this physiological and biochemical response of *Mesophellia* fruit-bodies to fire. They collected specimens of *Mesophellia glauca* from unburnt sites and sites burnt at various intensities. In the field it was noticeable that fruit-bodies collected from burnt sites had different odours to fruit-bodies collected in unburnt sites. Fruit-bodies, collected from sites where the fire had reached its hottest intensity, had developed a strong odour that resembled rotting onions. In places the odour was so intense that it permeated the soil profile. This odour was less apparent in fruit-bodies collected from sites where the fire had burnt at a lower intensity, and it was absent in fruit-bodies collected in unburnt sites. Fruit-bodies collected at the latter sites tended to have a faint fruity or nutty odour.

J.M. Trappe (unpublished data) has seen a similar response of *Mesophellia ingratisima*: specimens from unburnt sites have a mild odour, those from burnt sites smell intensely of rotten onions. This feature led Berkeley (1881) to coin its species name (*ingratisima* = 'most unpleasant'). Millington *et al.* (1997) heated fresh *Mesophellia* specimens and found that the odour changed and intensified. The volatiles, as analysed by gas chromatography, changed notably at temperatures of 40° C and above. These changes reflect the alteration of aromatic compounds in non-heated specimens to pyrolysis products in the heated ones, a phenomenon that also occurs when the European Perigord Black Truffle *Tuber melanosporum* is canned (L. Libby, Oregon State University, Department of Food Science, personal communication, 1990).

Based on our field observations and the work of Millington *et al.* (1997), we hypothesise that fire alters the volatile chemistry of hypogeous fruit-bodies of *Mesophellia*, making them more aromatic and therefore easier to locate by mammal mycophagists and perhaps increasing their attractiveness. Odours are the key indicator of these fungi for animals such as bettongs (Donaldson and Stoddart 1994). This phenomenon easily accounts for the observations that digging by mycophagous mammals increases quickly in recently burnt areas. Within the burnt area of the study site of Millington *et al.* (1997), the level of foraging activity by the Long-nosed Bandicoot *Perameles nasuta*, a known mycophagist (Claridge 1993), far surpassed its foraging in the adjacent unburnt area. Many of the forage-diggings left by bandicoots in the burnt area were identified as being made shortly after the fire, because they were quite weathered by the time of sampling some weeks later (A.W. Claridge, unpublished observations).

'Fire-adapted' or 'fire-dependent'?

Regardless of whether or not fire stimulates increased production of fruit-bodies by *Mesophellia*, there is no evidence that mycophagous mammals benefit either nutritionally or physiologically, in either the short or long-term, relative to animals feeding on fungi in unburnt habitats. This view is supported by the fact that the body condition and breeding capacity of adults, and the growth rates of pouch young of mycophagous bettongs in recently burnt habitats, does not differ significantly from that of animals in unburnt habitats (Johnson 1995; Vernes and



1. Charred peridium. 2. Spore mass. 3. Columella or sterile core

Figure 2. Fruit-bodies of *Mesophellia* from a burnt site, cross-sections of two specimens shown. These specimens had a strong odour combination of smoke with rotting onions.

Pope 2001). At least for bettongs, this would imply that fire has no effect, leading some authors to the conclusion that such animals are 'fire-adapted.' Such a conclusion seems more tenable than that of Taylor (1991, 1992), who considered they are 'fire-dependent.' Either way, mycophagous mammals such as bandicoots and potoroos depend on dense ground cover for shelter and predator avoidance (Claridge and Barry 2000). By reducing that ground cover, fire damages the habitat for these animals regardless of its effects on fruiting of fungi.

Benefits to *Mesophellia* of being consumed and dispersed immediately post-fire

Maser *et al.* (1978), Trappe and Maser (1979), and others detail the dispersal benefits to the fungus of being found, dug-up and consumed by a mycophagous mammal. Taylor (1991) emphasises its special importance immediately post-fire. Spores from the eaten fruit-bodies pass through the digestive tract of the animal intact and are voided in the faeces at some other location in that animal's home range. In addition, spores may be liberated *in situ* as the animal breaks open and discards the outer portion of the fungus as it feeds on the inner core or gleba (Claridge and May 1994). Dispersed spores may then germinate when conditions are appropriate and subsequently form new mycorrhizal colonies, or add to pre-existing ones, where suitable plant hosts are available (Lamont *et al.* 1985; Claridge *et al.* 1992; Lamont 1995). Forming new mycorrhizal colonies post-disturbance may be important for both fungus and tree host, because existing colonies of many mycorrhizal fungi may be reduced or killed by the fire (Malajczuk and Hingston 1981). In addition, quickly re-establishing mycorrhizal colonies may help the fungus become dominant in the post-fire plant/fungal succession (Claridge *et al.* 1993b,c). The fruit-bodies of *Mesophellia* may act as an 'escape pod' for that fungus, with its special adaptations of a hard, outer peridium and production deep enough in the soil to escape heat damage. Spores in specimens close to the surface are likely killed by heat, but the intensified odour of heated specimens would attract animals, which then could excavate the underlying, undamaged specimens and thus still disperse viable spores.

Hypothesis transformed to 'fact'

Taylor's (1991, 1992) hypothesis that fire stimulates fruit-body formation by *Mesophellia* spp., and is therefore beneficial for mycophagous mammals, appears to have been misapplied. For example, Taylor (1993a, p. 708) wrote, "Fire can play an important role in determining the carrying capacity of an area for bettongs. Areas with dense undergrowth can be opened up by the use of cool burning and made suitable for bettongs. Fire has also been found to stimulate the production of fruit-bodies by mycorrhizal fungi and thus can lead to increased food supplies (Taylor 1991; Taylor 1992)" (Taylor 1993a, p. 708). Taylor (1993b, p. 93) also wrote that, "The only example of a major shift in location of a home range between months was for an individual that moved into an area that was recently burnt. The home ranges of

other animals tracked at this time already included the burnt area. Fungal fruit-bodies are much more abundant in burnt areas (Taylor 1991, 1992) and thus this extension of home range would have been to take advantage of a localised increase in food abundance."

In our opinion, stating that 'fungal fruit-bodies are much more abundant in burnt areas', misinterprets a highly complex ecological phenomenon. What disturbs us most is this idea is likely to have an adverse impact on the management practices in areas occupied by mycophagous mammals. For example, the first comprehensive management strategy for the Tasmanian Bettong, as detailed in a Tasmania-wide management plan for the species (Driessen *et al.* 1990), refer to Taylor (1991) in stating that (p. 100-101), "Fire is a relatively common event throughout the bettong range. It is an integral part of bettong habitat as it helps to maintain an open understorey. This is particularly the case in scrubby and dense communities where, in the absence of fire, the understorey is likely to become dense and unsuitable for the bettong. In addition there is evidence to suggest that firing promotes the fruiting of mycorrhizal fungi which form the bulk of the diet of the bettong ..."

Prescribed fire may maintain open habitat for the Tasmanian Bettong, which prefers sites with little understorey vegetation (Taylor 1988; Driessen *et al.* 1990). However, some habitats are open regardless of time since the last fire, presumably because of poor soil fertility and low rainfall (Johnson 1995). To base management prescriptions on one small study (Taylor 1991) and promote prescribed burning with a notion that fire stimulates production of hypogeous fruit-bodies, with proportional benefit to the animals, is inappropriate. This is evident from the extensive study of the distribution of the Tasmanian Bettong by Driessen *et al.* (1990). They found no correlation between time since last fire and the relative abundance (as adjudged by forage-diggings) of the species (Driessen *et al.* 1990, p. 79). The interrelationship between the animal, its food resource and fire is less clear than appears in Taylor's papers (1991, 1992, 1993a,b). Accordingly, we cannot support the proposition that frequent fire is integral to maintaining viable populations of the Tasmanian Bettong through increased fungal production (Driessen *et al.* 1990).

Taylor's (1991) hypothesis has also been used in support of prescribed burning for management of mycophagous mammals in mainland south-eastern Australia. In the case of the endangered Long-footed Potoroo *Potorous longipes* in New South Wales, the local forest management authority, State Forests of New South Wales, stated in an Environmental Impact Statement (EIS) that, "Taylor (1991), for bettongs and Christensen and Maisey (1987) for Woylies (*B. penicillata*), stress the importance of fire in maintaining habitat for small macropods dependent on an underground fungal food resource" (Forestry Commission of New South Wales 1992, p. 99). Without further justification, the EIS then states in relation to *P. longipes*, that "Fire undoubtedly plays an integral role in the life-cycle of this species and in the distribution and abundance of its primary food source, underground-fruiting fungi."

Fire may well have played a role in shaping the past and present distribution of both the Long-footed Potoroo and its primary food resource, but that role remains to be defined. Fire could be detrimental to the species in the short-term, because it reduces the dense understorey cover that provides shelter from predators (Claridge and Barry 2000). Unlike the Tasmanian Bettong, the Long-footed Potoroo and the related Long-nosed Potoroo *P. tridactylus* do not typically occupy open habitat (Seebeck 1981; Scotts and Seebeck 1989; Bennett 1993; Claridge and Barry 2000). The response of forest-dwelling mammals to fire needs to be understood in terms of changes to both food and habitat resources (Claridge 1992).

The critical role of fire in maintaining fungal productivity has also been alluded to in management plans associated with the Northern Bettong *Bettongia tropica* in tropical Queensland. For example, Dennis (2001) stated, on the basis of the research work by Vernes (1998; 2000), that "...certain species of truffle responded by producing a greater biomass of fruit shortly after fire", and then later that, "To maintain appropriate vegetation structure and truffle abundance fires are a necessary management tool". While the role of fire in influencing vegetation patterns within the habitat of the species is (relatively) well understood (see Harrington and Sanderson 1994), so far there have been no studies to demonstrate that fire *per se* is necessary to 'maintain truffle abundance'.

Future studies

We propose that efforts should be made to better understand natural variation in the productivity of hypogeous fungi such as *Mesophellia* spp within and between forest and woodland sites. Benchmarks for such natural variation need to be established before one can speculate as to where fire is necessary for maintaining the productivity of hypogeous fungal communities. Even in the improbable event that fire stimulates *Mesophellia* to fruit, is such peak production really peak or merely at one end of a natural productivity continuum?

An equally worthy endeavour would be to further examine the volatile chemistry of *Mesophellia* fruit-bodies from burnt and unburnt areas. Although differences in the range

and concentration of volatile compounds in fruit-bodies have already been identified (Millington *et al.* 1997), the particular compound(s) responsible for the unique odour of these fruit-bodies remains to be identified. Further, we have not as yet established that mycophagous mammals respond to that odour. Observations on the foraging activity of diverse mycophagous mammals at burnt sites (Claridge 1992; Claridge *et al.* 2001) support the hypothesis that the fruit-bodies become more attractive to the animals post-fire. Once the compound(s) responsible for the odour of fruit-bodies from burnt areas are identified, they could be tested as attractants on laboratory and/or wild populations of mycophagous mammals with techniques such as presented by Donaldson and Stoddart (1994). The notion that simply stimulating *Mesophellia* fruit-body production will routinely benefit mycophagous mammals is compromised by field and laboratory-based observations that otherwise indicate such animals require a diverse fungal food base to achieve optimal nutritional benefit (e.g. Claridge and Cork 1994; Claridge *et al.* 1999). Studies on exactly why mycophagous mammals choose to utilise many species of fungi at any one time rather than just a few species would be also worthwhile.

Concluding remarks

The uncritical acceptance of Taylor's (1991) suggestion that fire stimulates rapid production of fruit-bodies of *Mesophellia* by some land management agencies that regularly use prescribed burning urgently needs to be re-examined. Well-designed experiments, both field- and laboratory-based, need to be conducted and solid information and understanding developed to replace the limited studies and views currently underlying prescribed burning regimes for the management of mycophagous mammals in Australian eucalypt forests and woodlands. Even if managers choose to use this now-dated view, it applies only to sites with Mesophelliaceae as significant components of the hypogeous fungal food base. The application to sites with otherwise few or no such fungi could potentially do more harm than good. To do more good than harm, forest managers need the facts that only a well designed and supported research program can provide on the fascinating interactions of hypogeous fungi, ground-dwelling mammals, habitat and fire.

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References

- Auld, T.D. and Bradstock, R.A. 1996. Soil temperatures after the passage of a fire: do they influence the germination of buried seeds? *Australian Journal of Ecology* **21**: 106-109.
- Berkeley, M.J. 1881. Australian fungi II. Received principally from Baron F. von Mueller. *Journal of the Linnaean Society of London* **18**: 386-387.
- Bennett, A.F. 1993. Microhabitat use by the long-nosed potoroo, *Potorous tridactylus*, and other small mammals in remnant forest vegetation of south-western Victoria. *Wildlife Research* **20**: 267-285.
- Bougher, N. and Lebel, T. 2001. Sequestrate (truffle-like) fungi of Australia and New Zealand. *Australian Systematic Botany* **14**: 1-47.

- Bradstock, R.A. and Auld, T.D. 1995.** Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* 32: 76-84.
- Bradstock, R.A., Auld, T.D., Ellis, M.E. and Cohn, J.S. 1992.** Soil temperatures during bushfires in semi-arid, mallee shrublands. *Australian Journal of Ecology* 17: 433-440.
- Christensen, P.E.S. 1980.** The biology of *Bettongia penicillata* (Gray 1837), and *Macropus eugenii* (Desmarest 1817) in relation to fire. Forest Department of Western Australia Technical Bulletin No. 91: 1-90.
- Christensen, P. and Maisey, K. 1987.** The use of fire as a management tool in fauna conservation reserves. Pp 323-329 in *Nature Conservation: the Role of Remnants of Native Vegetation*, edited by D.A Saunders, G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins. Surrey Beatty and Sons, Chipping Norton, NSW.
- Claridge, A.W. 1992.** Is the relationship among mycophagous marsupials, mycorrhizal fungi and plants dependent on fire? *Australian Journal of Ecology* 17: 223-225.
- Claridge, A.W. 1993.** Fungal diet of the long-nosed bandicoot (*Perameles nasuta*) in south-eastern Australia. *The Victorian Naturalist* 110: 91-95.
- Claridge, A.W. 2002.** Ecological role of hypogeous ectomycorrhizal fungi in Australian forests and woodlands. *Plant and Soil* 244: 291-305.
- Claridge, A.W., and Barry, S.C. 2000.** Factors influencing the distribution of medium-sized ground-dwelling mammals in south-eastern mainland Australia. *Austral Ecology* 25: 676-688.
- Claridge, A.W., Barry, S.C., Cork, S.J., and Trappe, J.M. 2000a.** Diversity and habitat relationships of hypogeous fungi. II. Factors influencing the occurrence and number of taxa. *Biodiversity and Conservation* 9: 175-199.
- Claridge, A.W., Cork, S.J., and Trappe, J.M. 2000b.** Diversity and habitat relationships of hypogeous fungi. I. Study design, sampling techniques and general survey results. *Biodiversity and Conservation* 9: 151-173.
- Claridge, A.W. and Cork, S.J. 1994.** Nutritional value of hypogeous fungal fruit-bodies for the long-nosed potoroo (*Potorous tridactylus*), a forest-dwelling mycophagous marsupial. *Australian Journal of Zoology* 42: 701-710.
- Claridge, A.W. and May, T.W. 1994.** Mycophagy among Australian mammals. *Australian Journal of Ecology* 19: 251-275.
- Claridge, A.W., Tanton, M.T., Seebeck, J.H., Cork, S.J. and Cunningham, R.B. 1992.** Establishment of ectomycorrhizae on the roots of two species of *Eucalyptus* from fungal spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylus*). *Australian Journal of Ecology* 17: 207-217.
- Claridge, A.W., Cunningham, R.B. and Tanton, M.T. 1993a.** Foraging patterns of the long-nosed potoroo (*Potorous tridactylus*) for hypogeous fungi in mixed-species and regrowth eucalypt forest stands in south-eastern Australia. *Forest Ecology and Management* 61: 75-90.
- Claridge, A.W., Robinson, A.P., Tanton, M.T. and Cunningham, R.B. 1993b.** Seasonal production of hypogeous fungal fruit-bodies in a mixed-species eucalypt forest stand in south-eastern Australia. *Australian Journal of Botany* 41: 145-167.
- Claridge, A.W., Tanton, M.T. and Cunningham, R.B. 1993c.** Hypogeous fungi in the diet of the long-nosed potoroo (*Potorous tridactylus*) in mixed-species and regrowth eucalypt forest stands in south-eastern Australia. *Wildlife Research* 20: 321-337.
- Claridge, A.W., Trappe, J.M. and Claridge, D.L. 2001.** Mycophagy by the swamp wallaby (*Wallabia bicolor*). *Wildlife Research* 28: 643-645.
- Claridge, A.W., Trappe, J.M., Cork, S.J. and Claridge, D.L. 1999.** Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungus. *Journal of Comparative Physiology B* 169: 172-178.
- Dell, B., Malajczuk, N., Grove, T.S. and Thomson, G. 1990.** Ectomycorrhiza formation in *Eucalyptus*. IV. Ectomycorrhizas in the fruit-bodies of the hypogeous fungi *Mesophellia* and *Castoreum* in eucalypt forests in Western Australia. *New Phytologist* 114: 449-456.
- Dennis, A.J. 2001.** Recovery Plan for the Northern Bettong (*Bettongia tropica*) 2000-2004. Report to Environment Australia, Canberra. Queensland National Parks and Wildlife Service, Brisbane.
- Donaldson, R. and Stoddart, M. 1994.** Detection of hypogeous fungi by Tasmanian bettong (*Bettongia gaimardi* Marsupialia: Macropodidae). *Journal of Chemical Ecology* 20: 1201-1207.
- Driessen, M.M., Hocking, G.J. and Beukers, P. 1990.** Habitat, Conservation Status and Management of the Tasmanian Bettong *Bettongia gaimardi*. Department of Parks, Wildlife and Heritage, Tasmania, 1-114.
- Fogel, R. 1976.** Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas Fir stand. *Canadian Journal of Botany* 54: 1152-1162.
- Forestry Commission of New South Wales 1992.** Proposed Forestry Operations in Eden Management Area: Supplementary Environmental Impact Statement. Forestry Commission of New South Wales, August 1992.
- Gardes, M. and Bruns, T.D. 1996.** Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Canadian Journal of Botany* 74: 1572-1583.
- Gardes, M., White, T.J., Fortin, J.A., Bruns, T.D. and Taylor, J.W. 1991.** Identification of indigenous and introduced symbiotic fungi in ectomycorrhizae by amplification of nuclear and mitochondrial ribosomal DNA. *Canadian Journal of Botany* 69: 180-190.
- Gomez, D.M., Anthony, R.G. and Trappe, J.M. 2003.** The influence of thinning on production of hypogeous fungus sporocarps in Douglas-fir forests in the northern Oregon Coast Range. *Northwest Science* 77: 308-319.
- Harrington, G.N. and Sanderson, K.D. 1994.** Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest. *Pacific Conservation Biology* 1: 319-327.
- Hunt, G.A. and Trappe, J.M. 1987.** Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. *Canadian Journal of Botany* 65: 438-445.
- Johnson, C.N. 1994a.** Fruiting of hypogeous fungi in dry sclerophyll forest in Tasmania, Australia: seasonal variation and annual production. *Mycological Research* 98:1173-1182.
- Johnson, C.N. 1994b.** Nutritional ecology of a mycophagous marsupial in relation to production of hypogeous fungi. *Ecology* 75: 2015-2021.
- Johnson, C.N. 1994c.** Mycophagy and spore dispersal by a rat-kangaroo: Consumption of ectomycorrhizal taxa in relation to their abundance. *Functional Ecology* 8: 464-468.
- Johnson, C.N. 1994d.** Distribution of feeding activity of the Tasmanian bettong (*Bettongia gaimardi*) in relation to vegetation patterns. *Wildlife Research* 21: 249-255.

- Johnson, C.N.** 1995. Interactions between fire, mycophagous mammals, and dispersal of ectomycorrhizal fungi in *Eucalyptus* forests. *Oecologia* **104**: 467-475.
- Lamont, B.B., Ralph, C.S. and Christensen, P.E.S.** 1985. Mycophagous marsupials as dispersal agents for ectomycorrhizal fungi on *Eucalyptus calophylla* and *Gastrolobium bilobum*. *New Phytologist* **100**: 93-104.
- Luoma, D., Trappe, J.M., Claridge, A.W., Jacobs, K.M. and Cázares, E.** 2003. Relationships among fungi and small mammals in forested ecosystems. In *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America* (C. J. Zable and R. G. Anthony eds). Cambridge University Press, New York Pp 343-373.
- Malajczuk, N., Trappe, J.M. and Molina, R.** 1987. Interrelationships among some ectomycorrhizal trees, hypogeous fungi, and small mammals: Western Australian and northwestern American parallels. *Australian Journal of Ecology* **12**: 53-55.
- Malajczuk, N. and Hingston, E.J.** 1981. Ectomycorrhizae associated with jarrah. *Australian Journal of Botany* **29**: 453-462.
- Maser, C., Trappe, J.M. and Nussbaum, R.A.** 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology* **59**: 799-809.
- Millington, S., Leach, D.N., Wyllie, S.G. and Claridge, A.W.** 1997. Aroma profile of the Australian truffle-like fungus *Mesophellia glauca*. Pp 331-342 in *Flavor Analysis - Developments in Isolation and Characterisation*, edited by C.J. Mussinana and M.J. Morello. American Chemical Society, Washington D.C.
- Monamy, V. and Fox, B.J.** 2000. Small mammal succession is determined by vegetation density rather than time since fire. *Austral Ecology* **25**: 580-587.
- Moore, D.** 1998. *Fungal Morphogenesis*. Cambridge University Press, Cambridge.
- Scotts, D. and Seebeck, J.H.** 1989. Ecology of *Potorous longipes* (Marsupialia: Potoroidae); and preliminary recommendations for management of its habitat in Victoria. Arthur Rylah Institute for Environmental Research Technical Report Series No. 62.
- Seebeck, J.H.** 1981. *Potorous tridactylus* (Kerr) (Marsupialia: Macropodidae): its distribution, status and habitat preferences in Victoria. *Australian Wildlife Research* **8**: 285-306.
- Stamets, P.** 2000. *Growing Gourmet and Medicinal Mushrooms*. 3rd Edition. Ten Speed Press, Berkeley. 574 pp.
- Taylor, R.J.** 1988. Ecology and Conservation of the Tasmanian Bettong (*Bettongia gaimardi*). Unpublished report to the Australian National Parks and Wildlife Service 126 pp.
- Taylor, R.J.** 1991. Plants, fungi and bettongs: a fire-dependent co-evolutionary relationship. *Australian Journal of Ecology* **16**: 409-411.
- Taylor, R.J.** 1992. Fire, mycorrhizal fungi and management of mycophagous marsupials: a reply. *Australian Journal of Ecology* **17**: 227-228.
- Taylor, R.J.** 1993a. Habitat requirements of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. *Wildlife Research* **20**: 699-710.
- Taylor, R.J.** 1993b. Home range, nest use and activity of the Tasmanian bettong *Bettongia gaimardi*. *Wildlife Research* **20**: 87-95.
- Trappe, J.M., Castellano, M.A. and Trappe, M.** 1992. Australasian truffle-like fungi. IV. *Malajczukia* gen. nov. (Basidiomycotina, Mesophelliaceae). *Australian Systematic Botany* **5**: 617-630.
- Trappe, J.M., Castellano, M.A. and Amaranthus, M.P.** 1996a. Australasian truffle-like fungi. VIII. *Gummiglobus* and *Andebbia* gen. nov. (Basidiomycotina, Mesophelliaceae) and a supplement to the Nomenclatural Bibliography of Basidiomycotina. *Australian Systematic Botany* **9**: 803-811.
- Trappe, J.M., Castellano, M.A. and Malajczuk, N.** 1996b. Australasian truffle-like fungi. VII. *Mesophellia* (Basidiomycotina, Mesophelliaceae). *Australian Systematic Botany* **9**: 773-802.
- Trappe, J.M., and Maser, C.** 1979. Ectomycorrhizal fungi: Interactions of mushrooms and truffles with beasts and trees. In *Mushrooms and Man: An Interdisciplinary Approach to Mycology* (T. Walters ed). Linn-Benton Community College, Albany, Oregon. Pp. 163-177.
- Vernes, K.** 1998. Ecology of the Northern Bettong (*Bettongia tropica*) in relation to fire. Report to Conservation Strategy Branch of the Department of Environment.
- Vernes, K.** 2000. Ecology of the northern bettong in fire prone wet sclerophyll forest. PhD Thesis, James Cook University of North Queensland, Townsville.
- Vernes, K. and Haydon, D.T.** 2001. Effect of fire on northern bettong (*Bettongia tropica*) foraging behaviour. *Austral Ecology* **26**: 649-59.
- Vernes, K. and Pope, L.C.** 2001. Stability of nest range, home range and movement of the northern bettong (*Bettongia tropica*) following moderate-intensity fire in a tropical woodland, north-eastern Queensland. *Wildlife Research* **28**: 141-50.
- Vernes, K., Castellano, M.A. and Johnson, C.N.** 2001. Effects of season and fire on the diversity of hypogeous fungi consumed by a tropical mycophagous marsupial. *Journal of Animal Ecology* **70**: 945-54.
- Weber, N.S.** 2002. Musings on "mushrooming." *McIlwainea* **13**: 63-76.