

THE SUNBIRD

Volume 27 No. 4

December 1997

AVIAN FRUGIVORY IN A SUBTROPICAL RAINFOREST: ELEVEN YEARS OF OBSERVATIONS IN LAMINGTON NATIONAL PARK

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ABSTRACT

Observations of fruit-eating by 21 bird species were made in a subtropical rainforest over an eleven year period from 1985 to 1995. The fruits of 125 plant species were utilised. Fruit feeding reached a peak from February to April and was lowest during the period from July to October, reflecting fruit availability. The greatest variety of fruits was eaten by Regent Bowerbirds and Lewin's Honeyeaters. The fruits visited by the greatest numbers of bird species were *Alphitonia excelsa*, *Ficus platypoda*, *Piper novae-hollandiae*, *Diploglottis australis*, *Polyscias elegans*, and *Elaeocarpus obovatus*. Predictability of fruiting and the use of fruits by various bird groups are discussed.

INTRODUCTION

Over two-thirds of Australian subtropical rainforest plants are fleshy fruited and, for this reason, are presumed to be bird-dispersed (Williams *et al.* 1984). In many cases, however, we do not know which fruits are actually eaten by birds, or which plant species are visited by which bird species. When such observations are recorded (e.g. Floyd 1989), it is usually not mentioned whether the birds make frequent or occasional use of the fruits.

Living at the edge of the continent's largest remaining tract of subtropical rainforest for more than a decade has given me an opportunity to record many observations and thus contribute to our store of knowledge on this subject. This paper presents a summary of these observations.

METHODS AND STUDY AREA

The study area comprises rainforest and edge habitat near Green Mountains, Lamington National Park (28°S, 153°E), close to and including the author's home

property at 740m asl. The fruiting seasons of trees, shrubs, vines and forbs and the birds visiting the fruiting plants were recorded over a period of eleven years (1985-1995). Feeding observations were recorded almost daily throughout this period, with notes being made of the species and locations of fruiting plants and the species of birds. Foraging methods and dates of observations were also noted. All yearly records of fruiting, and most monthly ones were made along a 5 km section of Lamington National Park Road, which traverses dry and subtropical rainforest and its peripheral areas.

Observations were mainly opportunistic, but trees seen in flower were noted and inspected periodically for commencement of fruiting. In addition, Regent Bowerbirds, Satin Bowerbirds and Green Catbirds were fed daily at our residence, and seeds in their faeces and in the drinking pool frequently gave an indication as to what plants to look for.

RESULTS

Birds eating fruits

One hundred and twenty-five species of fruits were seen to be consumed by the thirteen most commonly observed species of frugivorous birds (Table 1). Visits by three other frugivorous and five primarily insectivorous birds are recorded in Table 2. Fruits eaten by the greatest numbers of bird species were: *Alphitonia excelsa*, *Ficus platypoda* var. *platypoda*, *Piper novae-hollandiae*, *Diploglottis australis*, *Polyscias elegans* and *Elaeocarpus obovatus* (10 to 20 species), followed by *Ficus macrophylla*, *Olea paniculata*, *Elattostachys xylocarpa*, *Diospyros pentamera*, *Ficus superba* var. *henneana* and *Guioa semiglaucia* (8 or 9 species).

Fruit-doves were collectively seen to eat the fruits of 33% of the observed plant species, and other common frugivores which are potential dispersers ate fruits from 56% of the plant species. Fruits of 52% of the plant species were eaten by birds known or assumed to be seed predators (Table 1), and 4% were eaten by birds that are primarily insectivorous (Table 2). Bird species eating the greatest variety of fruits were Regent Bowerbird (70 species), Lewin's Honeyeater (60 species) and Satin Bowerbird (55 species).

Yearly and seasonal fruiting records of some important food plants
Dendrocnide excelsa, a common tree in the area, produces male and female flowers on separate trees. Crops of the pink fruit are produced in the late autumn and winter and fruiting appeared to be correlated with autumn weather conditions. No fruit was observed on trees during 1986, 1991 or 1994 when very dry conditions prevailed during autumn and early winter. Trees also failed to fruit in 1989 after high rainfall in April (752 mm). The five fruit-doves and Australian King-Parrot were never observed eating the fruit, but Wonga Pigeons ate fruit off fallen bunches on the ground.

TABLE 1. Fruits eaten by the most common frugivores. Numbers refer to months (1=January, 2=February, etc.). Each 'occ' indicates that only one or two observations were made for any particular plant. Life form: T=trees, TS=tall shrub, S=shrub, LS=low shrub, V=vine, P=parasite, F=forb, G=graminoid. * =naturalised species. LH=Lewin's Honeyeater, S=Silvereye, PR=Paradise Riflebird, GC=Green Catbird, RB=Regent Bowerbird, SB=Satin Bowerbird, RCFD=Rose-crowned Fruit-Dove, W=Wompoo Fruit-Dove, TP=Topknot Pigeon, BCD=Brown Cuckoo-Dove, WHP=White-headed Pigeon, CR=Crimson Rosella, KP=King Parrot.

Species	Life Form	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WHP	CR	KP
DICOTYLEDONS														
Akania bidwillii	T	4					4							
Alangiaceae	T						1,2	1		2,3	1,2	2		
<i>Alangium villosum</i> subsp. <i>polyosmoides</i>	T												1	1,2
Anarcardiaceae	T	1,2	1				1,2	1,2						
<i>Euroschinus falcata</i>	LS						1,2	1,2	8					
Apocynaceae	V							6 occ					6	4-7
<i>Carissa ovata</i>	T	4-7	4-7	5-7	4-8	4-8	5-7						6	3,4
Araliaceae	T													
<i>Cephalalaria cephalobotrys</i>	V													
<i>Polyscias elegans</i>														
<i>Polyscias murrayi</i>														
Celastraceae	V	5,6	5											
<i>Celastrus subspicata</i>	V													
Cucurbitaceae	V													
<i>Diplocyclos palmatus</i>	V													
<i>Sicyos australis</i>	V													
<i>Zehneria cunninghamii</i>	V	5											2,4	

Species	Life Form	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WHP	CR	KP
DICOTYLEDONS (cont.)														
Dilleniaceae														
<i>Hibbertia scandens</i>	V													
Ebenaceae	T	6 occ												
<i>Diospyros australis</i>	T	1												
<i>Diospyros pentamera</i>					1-3,9, 11,12	1-3,8 11,12	1,2,3, 12	1,2,12	2,3,12	1,12				11
Ehretiaceae	T	2-4				2	2-4	2	2					
<i>Ehretia acuminata</i>														
Elaeocarpaceae	T	2-6			3	11	2-5	2-5	3	2-4				
<i>Elaeocarpus kirtonii</i>	T													
<i>Elaeocarpus obovatus</i>														
Euphorbiaceae	T													
<i>Baloghia inophylla</i>	T													
<i>Brennia oblongifolia</i>	T	2,3												
<i>Claorylon australe</i>	T													
<i>Cleistanthus cunninghamii</i>	T	5		1										
<i>Drypetes deplanchei</i>	S	1,2												
<i>Omalanthus nutans</i>														
Flacourtiaceae	T	4occ												
<i>Casearia multinervosa</i>	T	2,3												
<i>Scopolia braunii</i>	T	2,3												
Icacinaceae	T													
<i>Pennantia cunninghamii</i>														
Lauraceae	T													
<i>Cinnamomum virens</i>														
<i>Cryptocarya bidwillii</i>	T													
<i>Cryptocarya erythroxylon</i>	T													
<i>Cryptocarya obovata</i>	T													

Species	Life Form	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WHP	CR	KP
DICOTYLEDONS (cont.)														
<i>Cryptocarya triplinervis</i>	T	3								3	3		2	3
<i>Litsea reticulata</i>	T					2	2			2		2	1,2	12
<i>Neolitsea australiensis</i>	T				5,6					7				
<i>Loganiaceae</i>														
<i>Strychnos axillaris</i>	T													
<i>Loranthaceae</i>	P													
<i>Amylotheca dictyophleba</i>														
<i>Meliaceae</i>	N	2			3	2,3	3-5	2-4	2,3	4				
<i>Anthocarapa nitidula</i>	T	3,4			3,4	3	3	3	3					
<i>Diospyrum fraserianum</i>	T	2			12	2,12								
<i>Diospyrum rufum</i>	T	5,6			5,6	6								
<i>Melia azedarach</i> var. <i>australisica</i>	T											4	4	
<i>Ovenia cependana</i>	T													
<i>Synoum glandulosum</i>	T													
<i>Menispermaceae</i>	V													
<i>Legnephora moorei</i>	V													
<i>Mimosaceae</i>	T	1,12	1,12	1,12										
<i>Acacia maidenii</i>	T													
<i>Moraceae</i>	T													
<i>Ficus coronata</i>	T	10,11				2,11	2,3,9-11	3,9-12						
<i>Ficus macrophylla</i>	T	1,10-12	1			11,12	1,10-12	1,9-12	1,12					
<i>Ficus platypoda</i> var. <i>platypoda</i>	T	3,6,9-12				3,6,9,	3,7,	1,3,						
<i>Ficus superba</i> var. <i>henneana</i>	T					10	9-12	7-12						
<i>Ficus watkinsiana</i>	T					1,2,5,	3,4	1-3,5,						
<i>Machura cochinchinensis</i>	V	2,3				10,11								
<i>Malaisia scandens</i>	V													
						2,11								
						2								

Species	Form	Life	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WHP	CR	KP
DICOTYLEDONS (cont.)															
<i>Streblus brunonianus</i>	T	2-4									1,2,4		2,6	1,4	
Myrsinaceae															
<i>Rapanea howittiana</i>	T	1	1					12	1						
Myrtaceae	T														
<i>Acmena ingens</i>	T					9				10	10				
<i>Acmena smithii</i>	T														
<i>Austromyrtus hillii</i>	T	3,4													
<i>Decaspermum humile</i>	T	8,11													
<i>Rhodamnia argentea</i>	T	4-7													
<i>Rhodamnia rubescens</i>	T														
<i>Rhodomyrtus psidioides</i>	T	6													
<i>Syzygium australe</i>	T	4													
<i>Syzygium crebrinerve</i>	T														
<i>Syzygium francisii</i>	T	5-7													
* <i>Syzygium paniculatum</i>	T														
<i>Tristaniopsis collina</i>	T														
Oleaceae	V														
<i>Jasminum dallachii</i>	V														
<i>Jasminum simplicifolium</i>	V														
subsp. <i>australiense</i>	T														
<i>Olea paniculata</i>															
Phytolacaceae	LS														
* <i>Phytolacca americana</i>	LS	2-4,6													
<i>Phytolacca octandra</i>		4													
Piperaceae		6													
<i>Piper novae-hollandiae</i>	V	1,2	1,2,12	2	1,2	1,2	1,2	1,2	1,2	1,2	1,2,12	11	1,2,11,12		
Pittosporaceae	T	5	4-6												
<i>Pittosporum undulatum</i>															
Polygonaceae															

Species	Life Form	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WHP	CR	KP
DICOTYLEDONS (cont.)														
<i>Muehlenbeckia gracillima</i>	V		4occ											
Rhamnaceae	T	1-4,12	1-4,12	3,12	11,12	1-3,12	2-4			12occ	2,12	10	1-4,7, 12	2-4,6,7, 9,12
<i>Alphitonia excelsa</i>												3	9	
<i>Emmenosperma alphitonioides</i>	T													6
Rosaceae	F	1,3												
* <i>Duchesnea indica</i>	LS	1,5,6												
<i>Rubus moluccanus</i>	V													
<i>Rubus moorei</i>	LS	10,11												
<i>Rubus rosifolius</i>														
Rubiaceae	V	2												
<i>Morinda jasminoidea</i>														
Rutaceae	T													
<i>Acronychia baierlenii</i>	T													
* <i>Acronychia oblongifolia</i>	T													
<i>Acronychia suberosa</i>	T													
* <i>Citrus limon</i>	T													
<i>Geijera salicifolia</i> var. <i>latifolia</i>	T													
<i>Halfordia kendack</i>	T													
<i>Melicope micrococca</i>	T													
<i>Pentaceras australe</i>	T													
<i>Sarcocelikoce simplicifolia</i>	T													
<i>Zanthoxylon brachyacanthum</i>	T	4occ												
Sapindaceae	T													
<i>Cupaniopsis flagelliformis</i>	T											3,5		
var. <i>australis</i>	T													
<i>Cupaniopsis foveolata</i>	T													
<i>Sarcopteryx stipata</i>	T	1,12	1,12	2							12	1,12	1,12	1,12

Species	Life Form	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WFP	CR	KP
DICOTYLEDONS (cont.)														
<i>Diploglottis australis</i>	T	12					12	1,12						
<i>Elatostachys xylocarpa</i>	T	4-6,10	4-6		4,5,7,10	1,12	5,7,10	4,5,10	1,12	1,12	12		1,12	
<i>Guioa semiglaucia</i>	T	2	2		2	2	2	2			4	2,6,10		2
<i>Jagera pseudorhus</i>	T	9-12			10-12		9-11	9-11			2			
<i>Mischocarpus anodontus</i>	T	4,5			4,5		4,5							
Sapotaceae														
<i>Planchonella myrsinoides</i>	T													
Simaroubaceae														
<i>Guilfoylia monostylis</i>	T													5,9
Solanaceae														
<i>Duboisia myoporoides</i>	T													
<i>*Physalis peruviana</i>	LS	4					11							
<i>Solanum aviculare</i>	S	1-3,5, 6,8					1-3	1-3,8	4,5					4,5,8
<i>*Solanum mauritianum</i>	S													
<i>*Solanum americanum</i>	F	3,5,7, 12	2,4,12					1,4,8, 12	8,9					
<i>*Solanum pseudocapsicum</i>	F													
Sterculiaceae														
<i>Brachychiton acerifolius</i>	T													
<i>Symplocaceae</i>	T													
<i>Symplocos thwaitesii</i>	T													
Thymelaeaceae														
<i>Phaleria chermsideana</i>	T													
<i>Pimelea neoanglica</i>	T													
Ulmaceae														
<i>Aphananthe philippinensis</i>	T													
														5
														4
														12

Species	Life Form	LH	S	PR	GC	RB	SB	RCFD	W	TP	BCD	WHP	CR	KP
DICOTYLEDONS (cont.)														
<i>Urticaceae</i>														
<i>Dendrocnide excelsa</i>	T	6,7	6	5-7	5-7	5-7	5-7	5-7	5-7	5-7	5-7	5-7	5-7	5-7
<i>Verbenaeeae</i>	S	1,4	1,4-7, 12				1	12					12	
<i>*Lantana camara</i>														
<i>Premna lignum-vitae</i>	T						10	11			11			
<i>Vitaceae</i>	V	2-6												
<i>Cayratia clematidea</i>	V	3				4	3	2,7,8	6-8	4	4	4	4	4
<i>Cayratia euryrema</i>	V					5-8							6	
<i>Cissus antarctica</i>	V													
<i>Cissus hypoglauca</i>	V	4				5,6	4-6	4-7		3-7	5-7			
<i>Tetrastigma nitens</i>	V												4	
MONOCOTYLEDONS														
<i>Agavaceae</i>	S	4,5												
<i>Cordyline petiolaris</i>	LS													
<i>Cordyline rubra</i>														
<i>Araceae</i>	V													
<i>Pothos longipes</i>	G	1,11,12	1,12											
<i>Liliaceae</i>	V													
<i>Dianella caerulea</i>														
<i>Philesiaceae</i>														
<i>Eustrephus latifolius</i>	V													

TABLE 2. Fruits eaten by birds that were seldom recorded consuming fruit in the study area.

Bird	Plant	Family	Month
Mistletoebird	<i>Cayratia clematidea</i>	Vitaceae	4
	<i>Rhodomyrtus psidioides</i>	Myrtaceae	6
	<i>Dendrocnide excelsa</i>	Urticaceae	6
	<i>Amylotheca dictyophleba</i>	Loranthaceae	3
	* <i>Cotoneaster glaucophylla</i>	Rosaceae	3
Common Koel	<i>Rubus rosifolius</i>	Rosaceae	11
	<i>Jagera pseudorhus</i>	Sapindaceae	11
	<i>Ficus superba</i> var. <i>henneana</i>	Moraceae	11
	<i>Ficus platypoda</i> var. <i>platypoda</i>	Moraceae	12
	<i>Ficus macrophylla</i>	Moraceae	2
Figbird	<i>Elaeocarpus obovatus</i>	Elaeocarpaceae	3
	<i>Ficus superba</i> var. <i>henneana</i>	Moraceae	12
	<i>Ficus platypoda</i> var. <i>platypoda</i>	Moraceae	10
	<i>Ficus macrophylla</i>	Moraceae	2,4
	<i>Ficus watkinsiana</i>	Moraceae	4
Varied Triller	<i>Olea paniculata</i>	Oleaceae	9,10
	<i>Melia azedarach</i> var. <i>australisica</i>	Meliaceae	6
	<i>Alphitonia excelsa</i>	Rhamnaceae	12
	<i>Ficus platypoda</i> var. <i>platypoda</i>	Moraceae	10
	<i>Polyscias elegans</i>	Araliaceae	9
Golden Whistler*	<i>Elattostachys xylocarpa</i>	Sapindaceae	5,6,7
	<i>Jagera pseudorhus</i>	Sapindaceae	11
Crested Shrike-tit*	<i>Elattostachys xylocarpa</i>	Sapindaceae	5,6,7
	<i>Sarcopteryx stipata</i>	Sapindaceae	12
	* <i>Physalis peruviana</i>	Solanaceae	5
	<i>Dianella caerulea</i>	Liliaceae	4
	* <i>Duchesnea indica</i>	Rosaceae	1

* Golden Whistler and Crested Shrike-tit consumed arils only after removing them from the seed.

The vine *Tetrastigma nitens* produced prolific crops during the autumn and winter months of 1986, 1987, 1991, 1992 and 1995. Flocks of Topknot Pigeons and small parties of Wompoo Fruit-Doves fed on the fruit for periods of up to two months. *Polyscias elegans* provided reliable autumn and winter crops, and most of the trees bore fruit annually from 1985 to 1995, even during dry periods. *Olea paniculata* was another important food source, but fruited irregularly during late winter and the spring of 1985, 1986, 1990, and 1992-1995. White-headed Pigeons and Regent Bowerbirds ate the green unripe fruit and King-Parrots stripped some trees of green fruit. *Elaeocarpus obovatus* carried ripe fruit for long periods in summer and autumn during 1987, 1990, 1992, 1993 and 1995. Ripe fruit occasionally remained on individual trees for weeks before any

feeding observations were made, although at other times the trees were very well visited by birds. Both large and small trees produced very large crops. Trees were situated at the forest edge or in open paddocks.

Four species of *Ficus* were utilised throughout each year, and fruit was available in any month of the year on at least one of the four species. However, more frequent crops were produced in spring and summer. *Ficus watkinsiana* is the most abundant fig in the area, while *F. macrophylla*, *F. platypoda* var. *platypoda* and *F. superba* var. *henneana* occur as occasional trees. *F. obliqua* was not located and only a few small trees of *F. coronata* and *F. fraseri* were noted.

The common vine *Piper novae-hollandiae* fruited in the spring and summer months of 1985, 1986, 1988-1991, 1993 and 1994, and its fruit was eaten in an unripe condition by White-headed Pigeons and Topknot Pigeons. *Diospyros pentamera* carried crops of ripe fruit in the spring and summer months of 1987-1988, 1988-1989, and 1993-1994. One tree under regular observation bore yellow fruit from May to September 1993, and ripe reddish fruit from October through to the following early February. Some fruit was seen to be eaten when yellow during August and September by Regent Bowerbirds and Green Catbirds. *Diploglottis australis* was popular when ripe crops were produced in the December - January period, although no fruit was produced in the summer seasons of 1986-1987, 1988-1989, 1990-1991 or 1993-1994. *Cryptocarya erythroxylon* is common in places above West Canungra Creek, and attracts large flocks of Topknot Pigeons whenever crops are produced in spring. *Pennantia cunninghamii* is found mainly along creek banks and in other moist situations; consequently only one small tree was found in the area under observation. Topknot Pigeons, Rose-crowned Fruit-Doves and Wompo Fruit-Doves are attracted to fruiting *Pennantia* trees in spring and summer.

Plants observed to have irregular or extended fruiting seasons

Olea paniculata fruited irregularly, but when crops were produced they provided a food source that was eaten in a green or ripe condition for periods of up to four months. Individual trees of *Ficus watkinsiana* and *F. superba* var. *henneana* fruited continuously for long periods and ripe fruit was usually available on some trees throughout the year. *Guilfoylia monostylis* produced large crops that remained in a ripe condition on some trees for six months or longer, although there was only a single occasion when fruit was observed being eaten (by a Green Catbird and a Satin Bowerbird). *Diospyros pentamera* bore crops on only three occasions during the study period, but some trees carried edible fruit that was utilised for periods of up to seven months. *Alphitonia excelsa* carried prolific crops in most years for periods of up to eight months. The fruit was consumed in a green condition by Green Catbirds, Crimson Rosellas and King-Parrots. *Rhodamnia argentea* had high visitation rates when trees fruited, but this occurred only in 1989 and 1993. Similarly, *Scolopia braunii* was popular during the fruiting events that occurred only in 1987, 1992 and 1993.

DISCUSSION

Fruit and bird groups

It is commonly suggested (e.g. Snow 1976) that the more highly frugivorous birds preferentially eat oil-rich fruits, whereas birds with a more varied diet eat the watery, carbohydrate-rich fruits. This is partially supported by the fact that all species of the oil-rich Lauraceae in the study were seen to be eaten by fruit-doves and more than half of them by bowerbirds. The oil-rich *Olea* was also eaten by fruit-doves and bowerbirds, and the two other Oleaceae fruits were eaten by bowerbirds. In contrast, only one Lauraceae and no Oleaceae were eaten by the more generalist Lewin's Honeyeater.

There was, however, much overlap and most plant families were utilised by a variety of birds. Over half of the fruit species were eaten by at least one seed predator, and eighteen species were seen to be eaten only by seed predators. The effect of these seed-digesting birds on the overall dispersal and survival of seeds of these species is as yet unknown. The encapsulated fruits of only one of the Sapindaceae species were eaten by fruit-doves, whereas fruits of all eight species were eaten by bowerbirds or Paradise Riflebirds, which probably have a greater manipulative ability (Beehler 1989).

Seasonality

The greatest diversity of fruit was available from late spring to early winter (June), especially from February to April. The bleakest season was from July to October. Some birds such as the Rose-crowned Fruit-Dove disappear from about May and reappear in spring, while White-headed Pigeons become locally nomadic. Topknot Pigeons become nomadic and Wompoo Fruit-Doves probably move to lower altitudes. However, at least some individuals of all common frugivores apart from the Rose-crowned Fruit-Dove and White-headed Pigeon were recorded in all or most months, in some years at least.

Fruits which are available from July to October are thus likely to be of considerable importance to frugivorous birds, especially to the obligate frugivores. Fruits that were seen to be eaten by seed-dispersing fruit-doves (and also by some bowerbirds) between July and October included *Tetrastigma nitens*, *Acronychia oblongifolia*, *Ficus macrophylla*, *F. platypoda*, *F. superba*, *F. watkinsiana*, *Acmena ingens*, *Jasminum dallachii*, *Olea paniculata* and *Neolitsea australiensis*. The eating of green fruits at times may indicate a certain degree of desperation by the birds because of a general lack of available fruit.

Fruits eaten by bowerbirds during this lean season, but not seen to be eaten by seed-dispersing fruit-doves, included *Polyscias elegans*, *Diospyros pentamera*, *Decaspermum humile*, *Rhodamnia argentea*, *Jasminum simplicifolium*, *Rubus rosifolius*, *Elattostachys xylocarpa*, *Jagera pseudorhus*, *Mischocarpus anodontus*,

Solanum aviculare, *Brachychiton acerifolius*, *B. discolor*, *Dendrocnide excelsa* and the introduced (from New South Wales) *Syzygium paniculatum*. The nectar of *Grevillea robusta* becomes an important food for Regent Bowerbirds (and to a lesser extent for Satin Bowerbirds) from July to December.

Given the variability in fruiting seasons and bird preferences, management plans for small reserves or forest restoration areas should consider the planting of a variety of local fleshy-fruited species, including some of the species with high visitation rates and some of those which fruit more or less reliably during the lean season.

ACKNOWLEDGEMENTS

My thanks to Ronda Green for her help and suggestions with the first draft of this paper. I am indebted to Bill McDonald for plant identifications over the years, to Peter O'Reilly for some feeding records, and to two anonymous referees for their helpful comments on the manuscript.

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