The bird communities of dry rainforests and surrounding woodlands in north Queensland

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ABSTRACT

Dry rainforest occurs throughout the wet-dry tropics as isolated patches in a matrix of savanna woodland. Dry rainforests may provide important stepping stones for migrating forest birds, resources for woodland birds, and a significant component of bird diversity in arid inland landscapes. Dry rainforest patches may provide both refuge from harsh environmental conditions and pulses of valuable resources not available in the less productive eucalypt woodland.

We investigated patterns of bird community composition and resource use in dry rainforest patches and adjacent eucalypt woodland in north Queensland. A preliminary aim was to describe the dry rainforest bird community and to then to assess the role of dry rainforest in the landscape, particularly to woodland birds.

Dry rainforest patches were found to have a distinctive bird community that rarely utilised resources in the surrounding eucalypt woodland. Thirteen bird species were characteristic of dry rainforest. Six of these were only ever recorded in dry rainforest. Woodland birds foraged in the dry rainforest, particularly during sporadic fruiting events. Bird density and species richness was higher in woodlands than dry rainforest.

Dry rainforest has a naturally patchy distribution and constitutes only 7% of the vegetation of the study region. The presence of this rainforest vegetation might buffer woodland vegetation from the long-term effects of drought by allowing the survival of bird pollinators during times of very low productivity in woodlands. Dry rainforests may also provide a refuge from fire, and resources immediately after fire when woodlands are burnt. If this unique vegetation type is to be conserved, active management is required to mitigate threats such as damage from cattle and feral pigs, weed invasion, fire and clearing.

Key words: dry rainforest, woodlands, drought, conservation and management

Introduction

Research on terrestrial bird communities in north-eastern Australia has tended to focus on complex wet rainforest which occurs in disjunct patches along the east coast (e.g. Crome 1978; Kikkawa 1982,1988; Frith 1984). The seasonally dry rainforests of inland Queensland have largely been ignored and little is known of their ecology or their role in the regional landscape. They are the least conserved and least ecologically well known of rainforest types (Kahn and Lawrie 1987). Since the ecological relationships of dry rainforest remain poorly understood, the role of these patches in the landscape, and their importance to both resident savanna and forest birds, as well as migrants, remains unknown. Studies elsewhere have shown that they provide refugia for a number of other vertebrate species (Horsup *et al.* 1993) and thereby add to regional biodiversity (Price *et al.* 1995).

Aims of this study

We studied the composition and dynamics of bird communities in a naturally patchy system of dry rainforest, within an extensive matrix of eucalypt woodland in the wet-dry tropics of northern Australia. The study was conducted at three dry rainforest sites (two basalt and one limestone) in the inland Townsville region of northern Queensland (*sensu* Kahn and Lawrie 1987). Specific questions addressed were:

- does dry rainforest support a discrete or specialised bird fauna?
- for what bird species are dry rainforests important?
- to what extent do savanna woodland birds utilise dry rainforests?

What is dry rainforest?

In the wet-dry tropics of Australia the climate is arid with permanently hot humid summers, warm dry winters and an annual rainfall of 600 – 1600 mm spread over 4 - 7 months. Rainfall, and thus soil moisture, is seasonal. The vegetation is dominated by savanna (Eucalypt) woodlands, with tall, closed, wet rainforest restricted to the humid east coast. In drier, sub-coastal areas these wet forests are replaced by patchily distributed, dry, closed canopy, deciduous forests, collectively known as dry rainforest. This apparently paradoxical term encompasses those rainforest formations that reflect a marked response to seasonal variability in rainfall. These include monsoon forests, brigalow, softwood

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scrubs, Araucarian vine thicket (hoop pine scrubs), and deciduous and semi-evergreen vine thickets (Gillison 1987). Other names colloquially attached to dry rainforests in Queensland include 'turkey scrubs', 'bastard scrubs', 'bottle-tree scrubs' and 'jungles'. Greenwood (1996) used 'monsoon forest' to encompass the "mostly to wholly deciduous 'dry rainforests' and 'vine thickets' of the wet-dry tropics of Australia". The term 'dry rainforest' is used throughout this paper to include all these variants.

In contrast to the sclerophyllous, mostly evergreen, woodland vegetation, dry rainforests are dominated by rainforest families such as Euphorbiaceae and Rubiaceae. They share many plant genera with complex wet rainforests of the east coast but are quite distinct at the species level, suggesting a long separate development (Gillison 1987). Dry rainforests are structurally different from wet coastal rainforests, having lower, more open, canopies and distinctive forms (e.g. bottle trees) and a deciduous phenology. They are characterised by a prickly, microphyll shrub layer and abundant vines and lianes. Most produce succulent or fleshy fruits that are attractive to birds and bats.

The vegetation, and thus the resources available to birds, in dry rainforests and woodlands differ substantially (Coughlan 2000). Eucalypt woodlands are dominated by eucalypts (*Corymbia/Eucalyptus* spp.) and Proteaceae (*Grevillea* and *Hakea* spp.) whose flowers provide a rich nectar source, but whose fruits are generally dry, woody capsules. Hence the woodland avifauna tends to be dominated by nomadic nectarivores that shift in response to flowering (Ford and Paton 1985). In contrast, many dry rainforest plants produce fleshy fruits and it follows that these patchy habitats may support a distinct avifauna dominated by frugivores, and may be an important resource for woodland birds and for migrating forest birds. These disjunct patches of closed canopy forest are tenuously connected, thus providing a continuity of rainforest habitat that may have great biological significance for migratory bird species (Kikkawa *et al.*1981).

Dry rainforest is often described as a depauperate form of rainforest and Kahn and Lawrie (1987) describe vine thickets as a 'poor cousin' in terms of structure, floristic and faunal complexity. Since dry rainforests are structurally simple in comparison with wet rainforests, we might expect the bird fauna of dry rainforests to be a depauperate sub-set of the moist/wet forest fauna.

Although some dry rainforest species are fire-tolerant and will regenerate after fire (Kahn and Lawrie 1987), they are generally fire-sensitive (Bowman 2000). Dry rainforests often grow in fire-protected situations such as rock outcrops, gullies and rocky substrates such as basalt and limestone. Ground cover is sparse, with abundant leaf litter and no grass layer. The closed canopy of dry rainforests restricts light reaching the forest floor and precludes growth of a ground layer so there is little build up of grassy fuel load. In comparison, eucalypt woodlands are well adapted to, and dependent on, the fires that result from high fuel loads (Ash 1988).

In Australia, dry rainforests occur in the Kimberley region of Western Australia (Clayton-Greene and Beard 1985), Cape York Peninsula (Kikkawa *et al.* 1981), the Northern Territory (Dunlop and Webb 1991), coastal and inland northern Queensland (Webb and Tracey 1981, Kahn and Lawrie 1987) and New South Wales (Floyd 1990). The extent of patches declines with distance from the coast and they do not occur where rainfall is less than about 500 mm per annum (Fensham 1995).

There has been much debate about the processes that have caused the present-day distribution of dry rainforest in Australia. One view is that dry rainforests were previously more widespread and have probably been present since the Cretaceous (135 mya) (Specht 1988) and that the current patchy distribution reflects the breakdown of extensive areas of dry rainforest by fire (Bowman 2000). Other factors posed to explain the current distribution patterns include soil fertility, soil moisture and Pleistocene climate changes (Webb and Tracey 1981, Kahn and Lawrie 1987, Russell-Smith 1991). However, there is also evidence that dry rainforest may be a 'weedy' vegetation type, opportunistically colonising fire-protected sites (Bowman 2000).

Threats to Dry Rainforest

Land clearance has had, and continues to have, a serious impact on dry rainforest. Fensham (1996b) estimated that 28.2% of the original extent of dry rainforest between latitudes 17°S and 23°S (encompassing our study area between 18°S and 20°S) has been cleared. Large patches have been preferentially cleared so most remaining patches are small (less than100 ha) (Fensham 1996b). A large proportion of extant dry rainforest in Queensland is reserved in national parks, but this is primarily in a few large reserves (Great Basalt Wall National Park, Toomba Basalt Flow and Forty Mile Scrub National Park).

The main threats to dry rainforest vegetation are the impact of feral animals, invasion of weeds and the resultant increased susceptibility to fire. The spread of the weed Lantana *Lantana camara* is particularly threatening as its proliferation in the understorey of dry rainforest increases the flammability of dry rainforest (Fensham 1996a, b). Structural alteration of the understorey caused by feral pigs and cattle is a precursor to this process. Although dry rainforests are not grazed, they are profoundly influenced by surrounding land use and there is a tendency for stock to use the patches as shelter, resulting in trampling of understorey shrubs and the invasion of exotic grasses and weeds (*pers. obs.*).

Summary of previous ecological research in dry rainforests

There is little published information on the fauna that use dry rainforests. Similarly, very little research has explored the relationship between dry rainforest and the savanna woodland vegetation that dominates Northern Australia, nor the ecological relationships of the animals that inhabit these patches. Research activity on birds in dry rainforest has predominantly come from the Northern Territory monsoon rainforest estate and included research at the community level (Woinarski *et al.* 1992, Woinarski 1993b) and on frugivory, seed dispersal and species area requirements (Price *et al.* 1999).

The monsoon rainforest estate of northern Australia (Russell-Smith 1991) is comparable to the dry rainforests of Queensland, in that patches of rainforest-related vegetation are embedded in a savanna-dominated landscape. The avifauna of monsoon rainforest patches in the Northern Territory and Cape York Peninsula is distinct from that of adjacent woodlands (Woinarski 1993b). While the species composition of these patches varies among monsoon forests of differing floristics or environment, they are more closely related to other monsoon rainforest patches in disjunct areas than to adjacent savanna habitats (Kikkawa *et al.* 1981).

In Queensland, the majority of work in dry rainforest is in the form of unpublished Queensland National Parks and Wildlife Service reports e.g. the Dalrymple and Einasleigh Fauna Surveys (Blackman *et al.* 1987), the University of New England Exploration Society surveys at Forty Mile Scrub (Stocker *et al.* 1961) and surveys at Barrabas Scrub (Stocker and Crome 1972). Although these surveys were never published and remain inaccessible, they are summarised in a review by Kahn and Lawrie (1987).

Methods

Site Selection

Replicate sites were selected to minimise variation in biogeographic factors such as patch size and distance from the coast. Thus the sites selected do not represent the full range of dry rainforest types in Queensland and the results may not be generalised for dry rainforests in different topographic, edaphic or floristic categories. The number of sites and their locations were chosen to allow regular sampling to capture seasonal and episodic fruiting and flowering events. Two dry rainforest patches were chosen at each of three study sites: Fanning River (19° 45', 146°27'), Rhonella Park (18° 41', 145° 20') and Meadowbank (18° 20', 145° 00') (Figure 1). The size of replicate patches (hectares) at each site was Meadowbank (16, 25), Rhonella Park (35, 39) and Fanning River (15, 21). Photos on this page show the nature of the boundary between dry rainforest and woodland at each of the sites. The photo on the next page shows the interior of dry rainforest at Meadowbank.

Boundary of dry rainforest on basalt soils at Meadowbank. Photo: J. Coughlan.

Boundary of dry rainforest on limestone at Fanning River. Photo: J. Coughlan.

Boundary of dry rainforest on basalt soils at Rhonella Photo: J. Coughlan.

Interior of dry rainforest at Meadowbank. Photo: J. Coughlan.

The entire study was conducted during a period of severe rainfall deficiency, with rainfall totals in the lowest 5% of historical totals across the region. The effect of cattle grazing and pigs was visible at all sites in this study and Lantana was present in all sites.

Bird Census

Bird censuses were conducted in dry rainforest patches and adjacent savanna woodland habitats at the three locations every second month from August 1993 to May 1995. At each location, a 1 km transect was placed in each habitat at each of two patches (two woodland and two dry rainforest transects at each site). Woodland transects were positioned 500 m from the edge of the dry rainforest to ensure that there was no influence of the dry rainforest habitat on the woodland census. Ten census points, each with a sampling radius of 20 m, were placed 100 m apart along each transect. Each census point was surveyed for 5 minutes. Birds of prey, nocturnal birds, waterbirds and extremely rare species that were seen on fewer than six occasions were excluded from quantitative analyses.

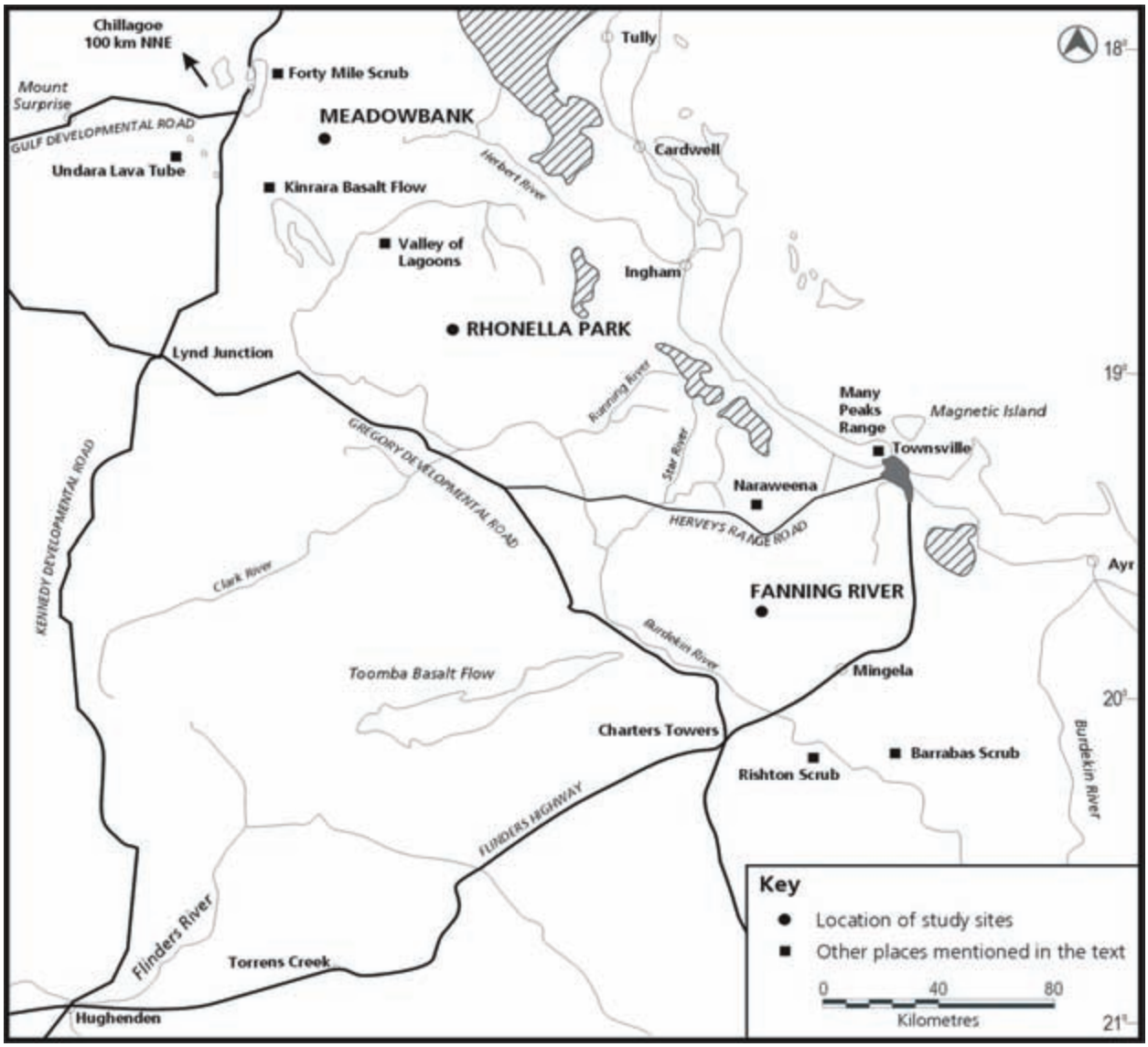

Figure 1. Location of study sites ● and other places mentioned in the text ■. Hatched areas show wet coastal rainforest.

Bird densities were calculated by dividing the mean transect abundance (means estimated from all trips and days for each transect) by the area of the transect (1.25 ha), which was the sum of the area of 10 census point circles. Densities are thus expressed as number of birds per hectare.

Foraging observations were made opportunistically during surveys. At each census point the species of tree in which birds were observed foraging was identified (or samples taken for subsequent identification); where possible it was noted whether each bird foraged on fruits, flowers, seeds or insects.

Principal components analysis

Principal components analysis was conducted on the covariance matrix (column centred) of the log (x+1) transformed abundances of species.

Indicator species analysis

Indicator species analysis was conducted in order to identify species that could be considered characteristic of particular habitats, sites or site groups within the study. An hierarchical cluster analysis using Ward's method and Manhattan (city block) distance was conducted on count data for 52 species (pooled over time) in order to determine the *a priori* groupings (clusters) of sites for which indicator species would be sought. Non-hierarchical classification (k-means) was then used to determine if any reallocation of sites to groups occurred. Since k-means classification is not constrained to produce hierarchical clusters, the actual presence of a hierarchical structure in the data can be verified (*i.e.* the stability of the hierarchical cluster solution is tested). The site groupings produced by k-means were then used as a basis for calculation of indicator values (*sensu* Dufrene and Legendre 1997) for all species within groups of the typology (level of clustering). The indicator value of a species is expressed as the degree (%) to which it fulfils the criteria of specificity and fidelity within any particular group of sites (McGeoch and Chown 1998) by combining relative abundance of a species with its frequency of occurrence in groups of sites. The indicator value is at a maximum when all individuals of a species are found in a single group of sites and all sites of that group. The indicator value of a given species is independent of the relative abundance of other species and in this sense this technique is superior to methods such as TWINSPAN devised by Hill (1979) for calculating indicator values. The statistical significance of a species indicator value was examined using a randomisation procedure and a t-test, to test whether the value for a species is significantly different from that expected from a random distribution of values. The results show whether a species' indicator value was significant for one or both tests. A species whose indicator value is above 55% for a particular site group is considered to be a true symmetrical indicator of that site group (*i.e.* its presence contributes to habitat specificity and one can predict its presence in all sites of that group). Species whose value is below 55% are considered asymmetrical (accidental or anecdotal) (Dufrene and Legendre 1997).

Results

Community composition

A total of 84 bird species belonging to 31 families were recorded from woodlands and dry rainforest patches at the three study sites (Table 1). Sixty-four species were recorded in dry rainforest and 74 in woodland. Fifty-two species were recorded from both habitats while 11 were recorded only in dry rainforest and 21 only in woodland.

The avifauna comprised 13 species of honeyeaters, 7 parrots and cockatoos, 6 cuckoos, 6 pigeons and doves, 6 birds of prey, 5 whistlers and flycatchers, 3 kingfishers, 2 cuckoo-shrikes, 2 butcherbirds, 2 fantails, 2 trillers and 30 single species groups. This included species that were variously sedentary, nomadic in response to flowering (mainly honeyeaters), summer breeding migrants from New Guinea and non-breeding winter migrants from southern temperate climates. The summer-breeding migrants – Common Koel, Dollarbird and Channel-billed Cuckoo – were generally absent from April to August and most commonly recorded during October to December. During that time, Common Koels and Channel-billed Cuckoos were frequently recorded in dry rainforest in the study area while Dollarbirds frequented the woodlands over summer. Non-breeding (winter) migrants from southern Australia (Morton and Brennan 1991, Kikkawa 1993) included the Leaden Flycatcher, Black-faced Cuckoo-shrike, Grey Fantail and Rainbow Bee-eater.

Red-backed Kingfishers, Diamond Doves and Little Button-quails, which are normally inhabitants of the arid inlands, but may move to the coast in drought years (Simpson and Day 1996, Woinarski and Tideman 1991), were only recorded in woodlands at Fanning River during the study.

Table 1. Species recorded from each site (Meadowbank = MB, Rhonella Park = RP, Fanning River =FR). Species are listed in taxonomic order following the convention of Christidis and Boles (1995). Common names and three-letter abbreviations are given for each species. Asterisks denote species recorded at least once at that site during the study.

Common name	Three letter code	Species Name	MB	RP	FR
Emu	EMU	*Dromaius novaehollandiae*	*		
Australian Brush-turkey	TKY	*Alecturi lathami*		*	*
Crested Hawk	CHK	*Aviceda subcristata*	*		
Whistling Kite	WKI	*Haliastur sphenurus*	*	*	
Grey Goshawk	GGH	*Accipiter novaehollandiae*	*		
Wedge-tailed Eagle	WTE	*Aquila audax*	*	*	*
Brown Falcon	FAL	*Falco berigora*	*	*	
Australian Kestrel	KES	*Falco cenchroides*	*		*
Brolga	BRO	*Grus rubicundus*			*

Common name	Three letter code	Species Name	MB	RP	FR
Little Button-quail	BUT	*Turnix velox*			*
Australian Bustard	KOR	*Ardeotis australis*		*	*
Common Bronzewing	CBW	*Phaps chaloptera*		*	
Crested Pigeon	CRP	*Ocyphaps lophotes*		*	*
Diamond Dove	DDV	*Geopelia cuneata*			*
Peaceful Dove	PCD	*Geopelia striata*	*	*	*
Bar-shouldered Dove	BSD	*Geopelia humeralis*		*	*
Squatter Pigeon	SQP	*Geophaps scripta*		*	
Red-tailed Black Cockatoo	RTB	*Calyptorhynchus banksii*	*		*
Sulphur-crested Cockatoo	SCC	*Cacatua galerita*	*	*	*
Cockatiel	CKT	*Nymphicus hollandicus*		*	*
Scaly-breasted Lorikeet	SBL	*Trichoglossus chlorolepidotus*	*	*	*
Rainbow Lorikeet	RBL	*Trichoglossus haematodus*	*	*	*
Red-winged Parrot	RWP	*Aprosmictus erythropterus*	*	*	*
Pale-headed Rosella	PHR	*Platycerus adscitus*	*	*	*
Oriental Cuckoo	ORC	*Cuculus saturatus*	*		
Fan-tailed Cuckoo	FTC	*Cacomantis flabelliformis*	*	*	
Horsfield's Bronze-cuckoo	HBC	*Chrysococcyx basalis*	*	*	*
Common Koel	KOE	*Eudynamys scolopacea*	*	*	*
Channel-billed Cuckoo	CBC	*Scythrops novaehollandiae*	*	*	*
Pheasant Coucal	PCL	*Centropus phasianinus*		*	*
Southern Boobook	BBO	*Ninox novaeseelandiae*	*		
Tawny Frogmouth	TFM	*Podargus strigoides*	*		
Laughing Kookaburra	LKB	*Dacelo novaeguineae*	*	*	*
Forest Kingfisher	FKF	*Todirhamphus macleayii*	*	*	
Red-backed Kingfisher	RBK	*Todirhamphus pyrrhopygia*			*
Rainbow Bee-eater	RBE	*Merops ornatus*		*	*
Dollarbird	DOB	*Eurystomus orientalis*	*	*	*
Striated Pardalote	STP	*Pardalotus striatus*	*	*	*
Weebill	WEE	*Smicrornis brevirostris*	*		*
Fairy Gerygone	FGY	*Gerygone palpebrosa*	*	*	
Noisy Friarbird	NFB	*Philemon corniculatus*	*	*	*
Little Friarbird	LFB	*Philemon citreogularis*	*	*	*
Blue-faced Honeyeater	BFH	*Entomyzon cyanotis*	*	*	*
Noisy Miner	MIN	*Manorina melanocephala*		*	*
Yellow-throated Miner	YTM	*Manorina flavigula*		*	*
Lewin's Honeyeater	LHE	*Meliphaga lewinii*	*	*	*
Black-chinned Honeyeater	BCH	*Melithreptus gularis*		*	
White-throated Honeyeater	WTH	*Melithreptus albogularis*	*	*	*
White-naped Honeyeater	WNH	*Melithreptus lunatus*		*	
Brown Honeyeater	BHE	*Lichmera indistincta*	*		*
Banded Honeyeater	BNH	*Certhionyx pectoralis*	*		
Dusky Honeyeater	DHE	*Myzomela obscura*	*		
Scarlet Honeyeater	SHE	*Myzomela sanguinolenta*	*		
Jacky Winter	JKW	*Microeca fascinans*			*
Grey-crowned Babbler	GCB	*Pomatostomus temporalis*			*
Rufous Whistler	RUF	*Pachycephala rufiventris*	*	*	*
Little Shrike-thrush	LST	*Colluricincla megarhyncha*	*		*
Grey Shrike-thrush	GST	*Colluricincla harmonica*			*
Leaden Flycatcher	LFC	*Myiagra rubecula*	*	*	*

Common name	Three letter code	Species Name	MB	RP	FR
Shining Flycatcher	SFC	*Myiagra alecto*			*
Magpie-lark	PEE	*Grallina cyanoleuca*	*	*	*
Rufous Fantail	RFT	*Rhipidura rufifrons*	*		
Grey Fantail	GFT	*Rhipidura fuliginosa*	*	*	*
Willie Wagtail	WAG	*Rhipidura leucophrys*	*		*
Spangled Drongo	DNG	*Dicrurus bracteatus*	*	*	*
Black-faced Cuckoo-shrike	BFC	*Coracina novaehollandiae*	*	*	*
White-bellied Cuckoo-Shrike	WBC	*Coracina papuensis*	*	*	*
Cicadabird	CIC	*Coracina tenuirostris*	*		*
White-winged Triller	WWT	*Lalage sueurii*			*
Varied Triller	VTR	*Lalage leucomela*	*	*	
Olive-backed Oriole	ORI	*Oriolus saggitatus*			*
Figbird	FIG	*Sphecotheres viridis*	*	*	
Black-faced Woodswallow	BFW	*Artamus cinereus*	*		*
Grey Butcherbird	GRB	*Cracticus torquatus*	*	*	*
Pied Butcherbird	PBB	*Cracticus nigrogularis*	*	*	*
Australian Magpie	MAG	*Gymnorhina tibicen*	*	*	*
Pied Currawong	CUR	*Strepera graculina*	*	*	*
Australian Raven	RAV	*Corvus coronoides*		*	
Torresian Crow	CRW	*Corvus orru*	*	*	*
White-winged Chough	WWC	*Corcorax melanorhamphos*			*
Apostlebird	APB	*Struthidea cinerea*			*
Great Bowerbird	GBB	*Chlamydera nuchalis*	*	*	*
Mistletoebird	MTB	*Dicaeum hirundinaceum*	*	*	*
Silvereye	SVE	*Zosterops lateralis*	*		

Bird density and species richness

Table 2 summarises species richness and density data for dry rainforest and woodland patches at each site. Bird species richness in dry rainforest was similar at all three sites (FR=42, MB=42, RP=38). Woodland species richness was more variable among sites (FR=53, MB=49, RP=43). On average, species richness in woodland was higher (mean = 48.3) than in dry rainforest (mean = 40.6).

Gradients in species composition

Figure 2 shows the species-site bi-plot produced by principal components analysis of species composition (abundance) data for sites on each trip. Locations are represented by symbol shape, and habitats by open or closed symbols. Since no strong temporal gradient was detected, trip numbers are not shown. The eight symbols for each location-habitat combination represent the eight

Table 2. Summary of species richness and density at all sites and habitats.

SITE	Habitat (patch)	Mean Bird Density (ha^{-1})		Species Richness	
		patch	habitat	patch	habitat
Fanning R.	Dry Rainforest (1)	5.5 ± 0.8	4.6 ± 0.6	32	42
	Dry Rainforest (2)	3.8 ± 0.8		29	
	Woodland(1)	17.7 ± 3.1	14.9 ± 1.8	41	53
	Woodland(2)	12.2 ± 1.9		42	
Meadowbank	Dry Rainforest (1)	15.4 ± 2.7	14.4 ± 1.6	30	42
	Dry Rainforest (2)	13.5 ± 1.9		39	
	Woodland(1)	17.9 ± 2.3	14.5 ±1.5	43	49
	Woodland(2)	10.6 ± 1.4		37	
Rhonella	Dry Rainforest (1)	7.3 ± 1.5	6.6 ± 0.9	32	38
	Dry Rainforest (2)	5.8 ± 1.2		31	
	Woodland(1)	13.15 ± 2.6	11.8 ± 1.7	33	43
	Woodland(2)	10.15 ± 2.1		35	

trips. Arrows in the diagram represent species, which are identified by their three-letter codes (see Table 1). The length of an arrow indicates the importance of that species. The angles between arrows represent the correlation between species and between the ordination axes. The first two principal components (axes) only explained 31% of the variance in the bird community. The first (horizontal) axis (17.5 % of variance) clearly represents a separation of sites based on habitats, with dry rainforest sites on the right of the plot and woodlands on the left. The second (vertical) axis (13.4 % of variance) suggests a gradient in species composition that relates to location, within each habitat, from Fanning River through to Rhonella Park to Meadowbank. The distinction between Fanning River and Rhonella Park was less in dry rainforest than in woodlands (*i.e.* black squares and circles are more closely clustered). The low overall variation accounted for by the two gradients can be explained by the inclusion of the temporal component (trip) which increased the inherent variation in the data set and revealed no strong gradient relative to the variation between habitats and sites. Subsequent axes individually explained only trivial variance (< 10% each).

Since temporal variations in species composition were small relative to the influence of habitat and location, the analysis was repeated with samples represented only by location and habitat. The resultant bi-plot is shown in Figure 3. The first two principal components explained 63% of variance in the species data (axis 1 = 37%, axis 2 = 26%). Species composition within a habitat at a given location showed little variation, with site scores lying close together. The exception was woodland sites at Meadowbank which appear to be twice as distant from each other as habitat pairs from other sites. The species composition of woodland bird communities appears to be more variable among sites, with a greater spread of points than dry rainforest. Eight species (Mistletoebird, Pied Currawong, Varied Triller, Great Bowerbird, Figbird, Fairy Gerygone, Lewin's Honeyeater and Grey Fantail) were closely aligned with the 'dry rainforest' axis. However, the position of the site scores suggests that it is species composition at Meadowbank sites that has the greatest influence on species scores (*i.e.* Meadowbank samples pull the arrow in that direction). A larger group of bird species appears on the left of the ordination diagram and is characteristic of woodlands at the three study sites. Six of these (Apostlebird, Yellow-throated Miner, Crested Pigeon, Cockatiel, Diamond Dove and Grey-crowned Babbler) were more characteristic of Fanning River woodlands, while species such as Rainbow Lorikeets, Scaly-breasted Lorikeets, White-throated Honeyeaters and Noisy Friarbirds were more characteristic of woodlands at Rhonella Park and Meadowbank.

The woodland avifauna overall was dominated by larger nectarivore/insectivore honeyeaters and parrots, and granivores (cockatoos) (mean weight of six most abundant = 102 g) whilst the dry rainforest was dominated by frugivores and smaller insectivores (mean weight of six most abundant = 50 g).

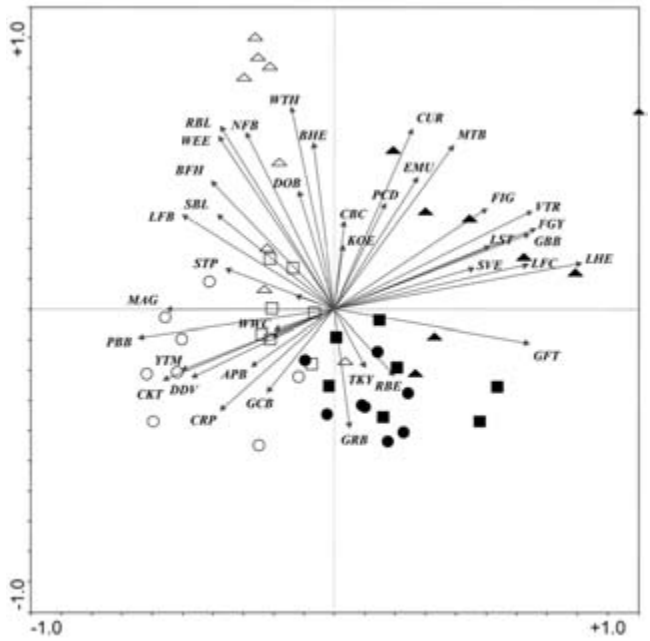

Figure 2. PCA Ordination diagram of bird count data for locations, habitats and trips. Abbreviations of species names are shown in Table 1. Closed symbols = dry rainforest sites, open symbols = woodland sites. Triangles = Meadowbank, squares = Rhonella Park, circles = Fanning River. Species whose scores lie close to the origin (0,0) are not represented on the diagram.

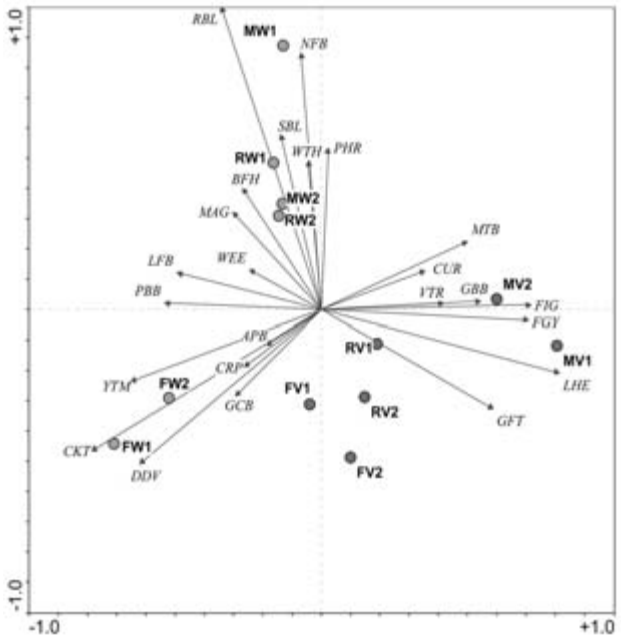

Figure 3. PCA ordination diagram of bird counts for sites and habitats. Abbreviations of species names are given in Table 5.2. Species are represented by arrows. Species whose scores lie close to the origin (0,0) are not represented on the diagram. FW = Fanning R. woodland; FV = Fanning R. dry rainforest (vine thicket); MW = Meadowbank woodland; MV = Meadowbank dry rainforest; RW = Rhonella Park woodland; RV= Rhonella Park dry rainforest. 1 and 2 are the replicate habitat patches at each site.

Indicator species analysis

Twenty-five bird species had indicator values greater than 55% (and were therefore considered symmetrical). Of these, 14 species were significant at the two-test level and a further 11 were significant at the one-test level. These species are shown in Table 3 along with their indicator values, significance levels and the habitat for which the species was a significant indicator.

Eight species were indicators of dry rainforest habitat, although two of these species (Figbird and Silvereye) were indicators of dry rainforest only at Meadowbank. Silvereyes only occurred at Meadowbank while Figbirds also occurred at Rhonella Park and were occasionally recorded from the woodlands at Meadowbank, but in much lower numbers. Those species that were best indicators of dry rainforest habitat overall were Fairy Gerygone, Great Bowerbird, Grey Fantail, Leaden Flycatcher, Lewin's Honeyeater and Australian Brush-turkey. Fairy Gerygones were absent from Fanning River and Brush Turkeys were absent from Meadowbank. The other species occurred at all three sites.

Seventeen species were indicators of woodland habitat. Nine were indicators of woodland overall (Blue-faced Honeyeater, Black-faced Cuckoo-shrike, Torresian Crow, Little Friarbird, Australian Magpie, Pied Butcherbird, Rainbow Lorikeet, Scaly-breasted Lorikeet, Striated Pardalote). Apostle Birds, Diamond Doves, Red-tailed Black Cockatoos and White-winged Choughs were indicator species for the site group produced by *k*-means clustering that only included the Fanning River woodland 1 transect. An indicator species for a single transect is meaningless and can be explained by the single occurrence of these species in high numbers on that transect and their absence from any other transect or site. It may also be explained by particular distribution patterns: for example, Townsville is the northern extent of occurrence of White-Winged Choughs. Three species (Cockatiel, Crested Pigeon and Australian Magpie-lark) were indicators of the woodland habitat at Fanning River although they also occurred in woodland habitat at other sites, but in much lower abundance. The Common Bronzewing was an indicator of woodland at Rhonella Park. Although it was recorded only in very low numbers there, it was not recorded at any other site.

Table 3. Significant Indicator Species for Woodland and Dry Rainforest Habitat.

Species	Indicator Value (%)	Habitat/Site	n	Frequency	Significance
Striated Pardalote	100	Woodland	45	6/6	**
Little Friarbird	87.1	Woodland	54	6/6	**
Pied Butcherbird	86.1	Woodland	62	6/6	**
Blue-faced Honeyeater	83.8	Woodland	57	6/6	**
Rainbow Lorikeet	81.3	Woodland	62	6/6	**
Torresian Crow	81.2	Woodland	52	6/6	**
Australian Magpie	80.5	Woodland	66	6/6	**
Black-faced Cuckoo-shrike	76.6	Woodland	36	6/6	**
Scaly-breasted Lorikeet	71.4	Woodland	66	5/6	**
Cockatiel	100	FR Woodland	83	2/2	*
White-winged Chough	100	FR Woodland	19	1/1	*
Australian Magpie-lark	83.3	FR Woodland	66	6/6	*
Crested Pigeon	79.9	FR Woodland	16	2/2	*
Common Bronzewing	85.7	RP Woodland	6	2/2	*
Apostlebird	100	FR Woodland (1)	11	1/1	*
Diamond Dove	97.8	FR Woodland (1)	76	1/1	**
Red-tailed Black Cockatoo	96.8	FR Woodland (1)	12	1/1	*
Lewin's Honeyeater	100	Dry Rainforest	68	6/6	**
Grey Fantail	87.6	Dry Rainforest	78	6/6	**
Leaden Flycatcher	77.8	Dry Rainforest	14	5/6	**
Great Bowerbird	70.2	Dry Rainforest	32	5/6	**
Fairy Gerygone	66.7	Dry Rainforest	48	4/6	*
Australian Brush-turkey	66.7	Dry Rainforest	11	4/6	*
Silvereye	100	MB Dry Rainforest	7	2/2	*
Figbird	92.2	MB Dry Rainforest	47	2/2	*

n = no. of individuals. Frequency = no. of sites in site group in which that species was present / number of sites in site group.
Significance: *= significant at one test level; **= significant at 2 test level.
RP = Rhonella Park. MB = Meadowbank. FR = Fanning River.
(1) = 1 of 2 transects in each habitat

Habitat fidelity

An indication of the habitat fidelity of each species is given by the proportion of observations of that species in each habitat. Species were ranked according to their Dry Rainforest Index (Table 4), which is the proportion of observations of a species in dry rainforest (range 0 - 1). Species with an index of 1.0 were never recorded in woodlands and were considered to be dry rainforest specialists. Species with an index of 0.0 were never recorded in dry rainforest and were considered to be woodland specialists. Birds in the top 20% of each habitat category were considered to favour that habitat (*i.e.* 0.0 - 0.2 woodland specialist, 0.8 -1.0 dry rainforest specialist). This index is based simply on a species' per cent occurrence in a habitat, and does not consider the abundance of each species, nor does it consider the number of sites at which the species was present. In this sense it is a coarse version of the indicator analysis and gives some insight into habitat preferences for those species whose abundance in a particular habitat was not high enough to result in a high indicator value. This analysis, based on simple per cent occurrences in each habitat, showed a group of 13 species to have high fidelity (>80%) to dry rainforest. Of these, six were recorded exclusively in dry rainforest habitat (Fairy Gerygone, Fantailed Cuckoo, Lewin's Honeyeater, Little Shrike-thrush, Silvereye and Brush Turkey). A larger group (21 species) showed high fidelity to woodland habitat. Seven of these (Black-faced Woodswallow, Cockatiel, Red-tailed Black Cockatoo, Striated Pardalote, Willie Wagtail, Weebill and White-winged Chough) displayed complete fidelity to the woodland habitat.

Table 4. Species' Dry Rainforest Index (see text for explanation). n = total no. of records.

Species	Proportion of records in dry rainforest	n	
Black-faced Woodswallow	0.0	6	
Cockatiel	0.0	92	
Red-tailed Black Cockatoo	0.0	24	
Striated Pardalote	0.0	25	
Willie Wagtail	0.0	5	
Weebill	0.0	46	
White-winged Chough	0.0	19	
Apostlebird	0.08	16	
Diamond Dove	0.08	107	
Yellow-throated Miner	0.08	76	
Common Bronzewing	0.09	11	Increasing Fidelity to
White-bellied Cuckoo-shrike	0.09	11	Woodlands
White-throated Honeyeater	0.12	42	
White-winged Triller	0.12	8	
Scaly-breasted Lorikeet	0.13	87	
Black-faced Cuckoo-shrike	0.14	36	
Little Friarbird	0.14	71	
Blue-faced Honeyeater	0.17	76	
Australian Magpie	0.17	95	
Rainbow Lorikeet	0.17	248	
Crested Pigeon	0.19	26	
Noisy Miner	0.25	146	
Torresian Crow	0.26	34	
Pied Butcherbird	0.27	83	
Noisy Friarbird	0.3	189	
Pale-headed Rosella	0.3	119	
Red-winged Parrot	0.3	17	
Dollarbird	0.31	19	
Brown Honeyeater	0.36	28	
Peaceful Dove	0.36	14	
Emu	0.38	13	
Grey-crowned Babbler	0.48	50	
Sulphur-crested Cockatoo	0.48	58	

Species	Proportion of records in dry rainforest	n	
Laughing Kookaburra	0.5	40	
Channel-billed Cuckoo	0.52	36	
Pied Currawong	0.58	41	
Rufous Whistler	0.6	44	
Rainbow Bee-eater	0.64	25	
Mistletoebird	0.66	56	
Bar-shouldered Dove	0.7	40	
Grey Butcherbird	0.7	47	
Common Koel	0.81	11	
Grey Fantail	0.83	110	
Varied Triller	0.84	32	
Spangled Drongo	0.88	18	
Leaden Flycatcher	0.9	19	
Figbird	0.91	47	Increasing Fidelity to
Great Bowerbird	0.96	48	Dry Rainforest
Fairy Gerygone	1.0	56	
Fantailed Cuckoo	1.0	9	
Lewin's Honeyeater	1.0	109	
Little Shrike-thrush	1.0	15	
Silvereye	1.0	7	
Australian Brush-turkey	1.0	16	

Table 5 shows the abundance and diversity of specialists for each habitat at each site. Fanning River had the highest diversity and abundance of woodland specialists and the lowest abundance of dry rainforest specialists. Meadowbank and Rhonella Park dry rainforest supported a similar number of dry rainforest specialists, but at Meadowbank they were five times as abundant. Dry rainforest specialists generally occurred in low abundances in woodland habitats. Meadowbank woodlands had three times as many dry rainforest specialists as the other sites, with abundances up to six times higher. Dry rainforest specialists were three times more abundant than woodland specialists in Rhonella Park dry rainforest and five times more abundant in Meadowbank dry rainforest. In contrast, Fanning River dry rainforests had similar numbers of woodland and dry rainforest specialists.

Foraging

Thirty-five bird species were observed foraging in the woodland during the study. Feeding on insects not associated with flowering of any particular plant species accounted for 46% of the records. A further 38% of records were associated with flowers of acacias, grevilleas, mistletoe, *Erythrina vespertilio*, *Melaleuca leucadendra* and eucalypts (*Eucalyptus*/*Corymbia* spp). Rainbow and Scaly-breasted Lorikeets and Noisy Friarbirds fed on the flowers of bloodwoods and ironbarks while insectivores such as the Jacky Winter, Striated Pardalote, White-throated Honeyeater, Noisy Miners and Yellow-throated Miners fed on insects attracted to the flowers. The remaining 16% of records were of foraging on fruits, seed and vertebrates. There were four records of feeding on seed from the ground (Bar-shouldered

Table 5. Abundance and species richness of habitat specialists in dry rainforest and woodland at the three study sites. Values are mean number of birds per transect over all trips. Dry rainforest specialists are those species whose dry rainforest index is >0.8. Woodland specialists are those species whose dry rainforest index is <0.2.

	Fanning River		Rhonella Park		Meadowbank	
	Dry Rainforest	Woodland	Dry Rainforest	Woodland	Dry Rainforest	Woodland
No. Dry Rainforest Specialists	9	2	11	2	12	6
Mean abundance	1.79	0.10	2.43	0.28	10.19	0.60
No. Woodland Specialists	10	9	8	11	6	13
Mean abundance	1.29	14.2	0.87	6.31	1.96	9.73

Dove, Common Bronzewing, Diamond Dove and Crested Pigeon). Frugivory was virtually absent in the woodland with the only fleshy fruit consumed being the grape-like fruit of the vine *Cayratia trifolia*, taken by Emus. Of the records from woodland, 94% were of woodland specialists. The Grey Fantail and the Varied Triller were the only dry rainforest specialists recorded foraging in the woodland.

Thirty-six species were recorded foraging on fruits, flowers, seeds and insects associated with 20 plant species in the dry rainforest during the study period. Fifty-two percent of foraging observations in dry rainforest were of 'woodland' birds. Twenty-three percent of observations were of feeding on flowers, probably nectar, of six plant species. Nectarivorous birds included five species of honeyeater, Little and Noisy Friarbird, Noisy Miner, Sulphur-crested Cockatoo and Rainbow Lorikeet. Flowering of *Brachychiton australis*, *Capparis* spp. and *Lysiphyllum hookeri* attracted insects that were fed upon by insectivores and omnivores. Insectivory accounted for 32% of foraging records and involved 17 bird species.

Frugivory contributed 37% of foraging records in dry rainforest, 54% of which were of foraging on figs. Sixteen species fed on fruits produced by 12 dry rainforest species. Fruit-bearing plants fed on by birds included *Briedelia leichhardtii, Melia azederach, Citriobatus spinescens, Diospyros humilis, Phyllanthus novaehollandiae, Flueggea virosa, Pleiogynum timorense* and *Ficus* spp.

The proportion of nectarivory observations was higher in woodland than dry rainforest, however dry rainforest had a greater diversity of birds feeding on flowers. The diversity of frugivores and the incidence of frugivory were markedly higher in dry rainforest than woodland. Insectivory made up a greater proportion of observations in woodland although the diversity of insectivores in the two habitats was similar. Species that fed on seeds in the woodland were all ground-foraging granivores of the family Columbidae. A more diverse avifauna fed on seeds of dry rainforest trees such as *Brachychiton australis, Geijera salicifolia* and *Briedelia leichhardtii*.

The dry rainforest bird community was dominated by frugivores and small insectivores while the woodland community was composed of nectarivores and larger insectivores (Coughlan 2000).

Discussion

The bird community

Dry Rainforest

This study has provided evidence for a distinct dry rainforest avifauna in isolated patches within a matrix of eucalypt-dominated savanna woodland. Ordination analyses revealed a gradient in species composition that separated woodland bird communities from dry rainforest bird communities. The dry rainforest bird community was a composite of forest and woodland birds, including a suite of forest generalists that had very high fidelity to dry rainforest. Woinarski (1993b) also found the monsoon rainforest bird communities in the Northern Territory to be a composite of woodland and rainforest birds. Those species with high fidelity to dry rainforest form a small subset of the rich coastal rainforest community. Indicator species analysis showed that six of these species were characteristic of dry rainforest across the region, while a few species were characteristic of dry rainforest at particular locations.

Cody (1993) noted that there is often a set of 'core' species in the assemblages of a particular habitat type that is constant, and species turnover is contributed mainly by rarer species that invade from adjacent habitats. Indicator species analysis showed that dry rainforest and woodland have quite different indicator species. Species indicative of dry rainforest habitat tended to be forest generalists, such as Lewin's Honeyeater, Australian Brush-turkey, Fairy Gerygone, Leaden Flycatcher and Grey Fantail. Fidelity analysis in each habitat showed a group of 13 species that had high fidelity (>80%) to dry rainforest with six species being confined to dry rainforest in the region. For both habitat types the indicator species formed a subset of the high fidelity species.

The number of dry rainforest specialists present at each site suggests that, within a vegetation type, structural or floristic variation can impact upon the composition of the avian community. The dry rainforest at Fanning River is drier, structurally depauperate and surrounded by much less rainforest habitat than the other two sites. Its dry rainforest is more open and more interdigitated with the surrounding woodland. As a result, the dry rainforest was used by more woodland birds and appeared less distinctly as a habitat for forest birds. It supported fewer dry rainforest specialists, but had many more woodland specialists. Some of the most abundant birds in dry rainforest at Fanning River were woodland specialists such as Pied Butcherbirds, Diamond Doves and Grey-crowned Babblers. The wetter, more complex dry rainforest at Meadowbank supported more dry rainforest specialist species in greater abundance. Two of the six most abundant species in dry rainforests at Fanning River and Rhonella Park were also among the six most abundant in woodland at those sites. In contrast, there was no overlap in the set of six most abundant species in dry rainforest and woodland at Meadowbank.

Regional similarities and differences in dry rainforest avifauna

Table 6 shows species found to be characteristic of dry rainforest in other studies. The Lewin's Honeyeater, Australian Brush-turkey and Grey Fantail were also among the most frequently recorded species in dry rainforests of south-east Queensland (Horsup *et al.* 1993). Stocker *et al.* (1961) recorded Lewin's Honeyeater as common in deciduous vine thicket at Forty Mile Scrub where it was the most prominent species.

Several species recorded exclusively in vine thickets in the inland Townsville region (Kahn and Lawrie 1987), were absent from dry rainforest sites in the current study (Brown Cuckoo-dove, Emerald Dove, White's Thrush, Variegated Fairy Wren, White-browed Scrubwren, Dusky Honeyeater). Of the 11 bird species found only in vine thicket, only two species (Silvereye and Australian Brush-turkey) were recorded in this study (both only in dry rainforest).

In surveys of vine thicket and adjacent woodland Dwyer (1972) found four species which occurred exclusively in vine thicket (Australian Brush-turkey, Lewin's Honeyeater, Grey Butcherbird and Brown Honeyeater). An additional five species were found in or adjacent to vine thicket, but not in woodland far from the vine thicket. He concluded that for these latter species the vine thicket was probably providing certain resources but was not the sole source of food.

Stocker *et al.* (1961) commonly found Noisy Friarbirds in the vine thicket at Forty Mile Scrub but never recorded them in the savanna woodland. In this study Noisy Friarbirds were the second most abundant bird overall in woodlands and fifth most abundant overall in dry rainforests. They were not abundant in Meadowbank dry rainforests (the site closest to Forty Mile Scrub) but were the second most abundant species in Meadowbank woodlands (Coughlan 2000).

Woodland

Woodland bird communities in this study were typical of northern Australian woodlands and were distinguished from dry rainforest bird communities. Twenty-one species showed high fidelity to woodland habitat; seven of these were only ever recorded in woodlands. All woodlands in this study were dominated by similar bird species, although Fanning River, the most southern and driest site, supported higher abundances of birds and a different species assemblage from those at Meadowbank and Rhonella Park.

Woodlands in this study had more species and more individuals than dry rainforest, which is not surprising given the absolute dominance of eucalypt woodlands as a vegetation type in tropical Australia relative to the small area and fragmented nature of dry rainforest in the study area and the region. Scattered and isolated patches of dry rainforest are probably too small to support distinct populations of forest birds and would not provide suitable foraging habitat for woodland specialists.

However, in comparison with dry rainforest communities, woodlands are more variable across the region. Australia's woodland avifauna is highly dependent on the dominant eucalypt vegetation. The two have evolved together as the continent has progressively become warmer and drier over the last 10 million years (Keast 1985). Woodlands are thus populated with nectar-dependent honeyeaters, pardalotes, which specialise on lerps and scales of eucalypt leaves, and lorikeets, also nectarivorous, which nest in hollow trunks and limbs of eucalypts.

Although considered aggressive invaders of disturbed edge habitats in south-east Queensland (Catterall 1993), Noisy Miners occurred as a normal component of the woodland avifauna in this study, in densities similar to other woodland specialists. Grey-crowned Babblers were a regular component of the woodland fauna at Fanning River but absent from the other two sites. Although commonly a woodland species (Blakers *et al.* 1984), they were the second most abundant species in dry rainforest at Fanning River. Grey-crowned Babblers were

Table 6. Comparison of characteristic dry rainforest bird species across studies. Characteristic species for this study are those with a dry rainforest index >0.8 or a significant indicator value for dry rainforest.

Species	This study	Kahn & Lawrie (1987)	Horsup *et al.* (1993)	Woinarski (1993b)	Dwyer (1972)
Lewin's Honeyeater	✔	✔	✔		✔
Grey Fantail	✔		✔		
Leaden Flycatcher	✔				
Great Bowerbird	✔				✔
Fairy Gerygone	✔	✔			
Australian Brush-turkey	✔	✔	✔		✔
Figbird	✔			✔	
Silvereye	✔	✔			
Little Shrike-thrush	✔		✔	✔	
Fantailed Cuckoo	✔		✔		
Spangled Drongo	✔		✔	✔	
Varied Triller	✔		✔	✔	
Common Koel	✔			✔	✔
Grey Butcherbird					✔
Rufous Fantail			✔	✔	
Emerald Dove		✔	✔	✔	
Yellow Oriole		✔		✔	

previously widespread throughout woodlands of eastern Australia. They are declining in New South Wales and southern Queensland due to habitat degradation of woodlands and have become extinct in South Australia and the ACT (Robinson and Traill 1996). In northern Queensland, dry rainforests may provide a refuge for this species and other woodland species that would be detrimentally affected by declines in area or quality of woodland habitat.

Comparisons of Species Richness in Dry Rainforest and Woodland

There are few published studies of dry rainforest bird fauna. Kahn and Lawrie (1987) have summarised the findings of the Dalrymple Fauna Survey (DFS) conducted in the inland Townsville region, which included several dry rainforest sites. The present study is comparable to the DFS since they were conducted in the same region over a similar geographic range and sampled a comparable number of sites. The intensity of sampling for the DFS is not known. Table 7 compares the numbers of species recorded in the DFS and the current study. The DFS reported a total of between 90 and 100 species for dry rainforest and contiguous woodland on a range of soil types. This is slightly higher than the 84 species we recorded in the region. Similar numbers of species were recorded exclusively in dry rainforest. Fifty-two species were recorded in both habitats in this study compared to 47 in the DFS. Dwyer (1972) found more species and more individuals in vine thicket (basalt scrub) than in surrounding woodland at sites near Mount Surprise.

Table 7. Comparisons of Bird Species Richness for Dry Rainforest and Woodland Habitats.

Recorded in:	This study	Dalrymple fauna survey*
Dry Rainforest	64	57
Woodland	74	80
Both habitats	52	47
Dry Rainforest only	11	10
Woodland only	21	33
Total	**84**	**90**

* data for soil-based Deciduous Vine Thicket (DVT) (Kahn and Lawrie 1987)

In the Northern Territory, specialised frugivores are concentrated in monsoon forests where fleshy fruited trees are relatively common (Morton and Brennan 1991) although Rose-crowned Fruit Doves are the only obligate frugivore to remain in the region throughout the year (Price *et al.* 1999). As is the case with dry rainforests in this study, these habitats supported fewer fruit doves and pigeons than the northern Queensland coastal rainforest. Absent from dry rainforest in this study were specialist fruit-eating pigeons such as Pied Imperial Pigeons that migrate to the Queensland coast and islands each year (Blakers *et al.* 1984). They are regular visitors to Northern Territory monsoon rainforests where they feed on fruits of the palm *Carpentaria acuminata* (Price *et al.* 1996). The absence of palms in inland dry rainforests may explain the absence of Pied Imperial Pigeons although they are capable of living and breeding in eucalypt woodland elsewhere (Blakers *et al.* 1984).

As plants bearing fleshy fruits are largely confined to rainforest vegetation types, and as frugivores are dependent on these fruits, the absence of specialised frugivores in dry rainforests suggests that the provision of fruit is inadequate to support populations of obligate frugivores. The abundance and regularity of fruit production in these highly seasonal and water-stressed forests is insufficient to sustain the diversity of frugivores seen in east coast wet forests.

It is likely that other dry rainforest patches in more favourable situations (e.g. coastal, higher elevation, higher rainfall) would have an even more distinct bird community, incorporating more rainforest specialists. This is the case in dry rainforest in south-eastern Queensland (Horsup *et al.* 1993) and other locations in north-eastern Queensland such as Magnetic Island and the Many Peaks Range, near Townsville (pers. obs.) and in monsoon rainforests in the Northern Territory (Price *et al.* 1996).

The Australian Brush-turkey, a mound building megapode, was absent from dry rainforest at Meadowbank and evidence of its decline in the region was seen at several sites. It occurs at Forty Mile Scrub, a large dry rainforest patch 40 km north-east of Meadowbank. At Fanning River, mounds were seen in exposed woodland situations, close to the edge of a dry rainforest patch. Assuming the mounds were built in the rainforest, this suggests rapid retraction of dry rainforest margins. Many abandoned/disused mounds were seen in dry rainforest at Rhonella Park suggesting that the patch had recently become sub-optimal habitat for the birds. Given that one of the colloquial names for dry rainforest or vine thicket is 'turkey scrub', dry rainforest has been important habitat for these sedentary forest birds in the past. Continual degradation of the habitat in inland Queensland may end this relationship, resulting in the disappearance of this species from inland rainforests and their extinction from the inland regions of Queensland.

The differences in bird community composition across dry rainforest sites in the inland Townsville region are not surprising given the high mobility of birds and the range of habitat types broadly considered under the 'vine thicket' or 'dry rainforest' umbrella. Differences between higher rainfall coastal vine thickets and drier arid inland vine thickets may be as great as between rainforest and woodland. Woinarski (1993b) showed that bird community composition in monsoon rainforest was re-arranged between monsoon rainforests of differing floristics and environment. Historical factors (biogeographic isolation) play a role in determining regional species diversity but environmental heterogeneity contributes much to local species diversity within each region. Vegetation structure, habitat area and contiguity, habitat patchiness and relative isolation, and the effects of history and chance all play a role in affecting diversity components in north eastern Australia (Cody 1993). Analysis of dry rainforest bird communities within pre-defined vegetation categories (such as the floristic sub-groups proposed by Fensham 1995), which take into account environmental heterogeneity within the dry rainforest estate, may show a clearer pattern in dry rainforest bird community composition.

In a survey of dry rainforest patches in south-eastern Queensland, Horsup *et al.* (1993) found on average 32 species per site, which is lower than the mean of 40 species in dry rainforests patches in this study. Kikkawa (1993) reported that lowland tropical rainforests supported the most diverse bird assemblages of closed forest types (100 species) followed by monsoon and gallery forest (96), tropical montane forest (71), and mangroves (62). Dry rainforests in this study supported 64 species.

Comparisons of bird density among vegetation types

Table 8 presents a summary of bird densities from various forest and woodland sites in Australia and New Guinea. Bird density in dry rainforest in this study was lower than that reported for the closed forests summarised in Woinarski and Tideman (1991) and monsoon rainforests in the Northern Territory (Woinarski *et al.* 1989). However, for woodlands in Victoria, MacNally (1996) has shown bird densities to vary substantially from year to year at a given site, with mean densities varying between seven and twelve birds per hectare over a three-year period. This makes among-habitat comparisons across studies difficult. Mean bird densities recorded in woodlands in this study were higher than those in Northern Territory woodlands (Woinarski and Tideman 1991). Dwyer (1972) suggested that patches of vine thicket act as features in the landscape, in a similar way to a spring or creek in an otherwise dry landscape, and hence provide a concentration of resources for birds to utilise. This is manifested in both greater species richness and higher abundances. Regarding the latter, Dwyer (1972) noted that the local abundance was increased near dry rainforest at Black Rock for some mobile woodland species that were otherwise more widely dispersed. However, in our study, density of woodland birds was highest at Fanning River where dry rainforest had the least distinct bird community and was less of a feature in the landscape. While surveys of woodland bird communities in the present study serve as a comparison with bird communities of adjacent dry rainforests, they are not necessarily representative of woodlands elsewhere in the region where dry rainforests are not a part of the landscape. Generalisations therefore cannot be made about the relative density of woodland birds in other northern Queensland woodlands.

Regional importance of dry rainforest

Dry rainforest supports populations of frugivorous birds that are vital to the process of seed dispersal and maintenance of floristic diversity of this vegetation type (Woinarski 1993b). Although woodlands in the region support more species and higher densities of birds than dry rainforests, dry rainforests add species to the regional/local pool that, in the absence of these forest isolates, would either not occur there or be irregular visitors. The dry rainforest bird community was dominated by frugivores and small insectivores while the woodland community was composed of nectarivores and larger insectivores (Coughlan 2000). Observations of foraging in this study showed that dry rainforest birds did not utilise the adjacent savanna but woodland birds foraged in the dry rainforest, particularly in response to sporadic fruiting events. Given the inter-dependence between nectar-feeders and bird-pollinated plants in northern Australian woodlands, dry rainforests may play a supportive role to the woodland avifauna in times of drought by providing supplementary resources. This might buffer woodland vegetation from the long-term effects of drought by allowing the survival of bird pollinators during times of very low productivity. Dry rainforests may also provide a refuge from fire, and resources immediately after fire when woodlands are burnt. However, given the small extent of the dry rainforest habitat relative to woodland in the region, the capacity of dry rainforest to buffer or provide refuge may not be significant.

The distinction between those species that rely on dry rainforest and those that are loosely and opportunistically associated with it is unclear and to some extent clouded by the drought conditions which prevailed during the present study. Under less severe conditions, dry rainforest may play a lesser role for opportunistic species seeking refuge from harsh conditions but a greater role for forest dependent birds and frugivores. It is clear, however, that the habitat is important for the survival of these species in the region.

Reductions in numbers of individuals and numbers of species during or after drought have been noted in several Australian studies. For eucalypt forests in central Queensland, Chan (1999) recorded fewer birds in a drought year than in a non-drought year and noted that fewer migrants frequented the area during the drought year. Recher and Holmes (1985) attributed

Table 8. Mean bird densities for various Australian vegetation types.

Bird Density (no/ha)	Vegetation Type	Study/Reference
5-15	Dry rainforest	This study
24-28	Monsoon rainforest (lowland)	Woinarski 1989
20.7	Tropical closed forest	*in* Woinarski & Tideman 1991
10.1	Tropical woodland	*in* Woinarski & Tideman 1991
12-15	Tropical woodland	This Study
12.0	Tropical open forest	*in* Woinarski & Tideman 1991
22.3	Temperate open forest	*in* Woinarski & Tideman 1991
18.1	Temperate woodland	*in* Woinarski & Tideman 1991

declines in bird numbers to poor reproductive success during a drought year and conversely suggested that above average rainfall in one year may have meant more favourable conditions for birds and resulted in the higher number of species seen in that year. Smith (1982) suggested that there were indirect effects of drought on a temperate avian community. She noted changes in breeding success, bird densities and trophic structure (decline in insectivores, loss of nectarivores, and increase in granivores). Reduced or erratic food supply may have been responsible for these effects on bird numbers although it is difficult to separate drought-induced variation in bird numbers and community structure from inherent variation in the community.

Dry rainforests in this study were used by mammals as shelter from temperature extremes and predators during the day (wallabies were seen taking refuge from Wedge-tailed Eagle pursuit). Swamp Wallabies *Wallabia bicolor* and Black-striped Wallabies *Macropus dorsalis* sheltered in dry rainforest during the day and foraged on the edge at night. Menkhorst and Woinarski (1992) found that there was no distinctive mammal fauna closely associated with monsoon rainforest in the northern Territory. No mammal species was restricted to monsoon rainforest; most were habitat generalists. They suggest that this lack of specialisation by mammals permits flexibility in the use of monsoon rainforests as a refuge on a seasonal or daily cycle. This may also be the case with birds. Although dry rainforests in this study had a bird fauna distinct from that of the surrounding savanna woodlands, most of the dry rainforest 'specialists' are forest generalists and occur in rainforest habitats elsewhere. Many are also species quite commonly recorded elsewhere in woodlands. For example, Chan (1999) recorded Spangled Drongos, Rainbow Bee-eaters, Lewin's Honeyeaters, Figbirds and Grey Fantails as a common component of the avifauna in a central Queensland Eucalypt woodland while in this study these species were almost exclusively recorded in dry rainforests. This could represent an opportunistic utilisation of a habitat by birds that would otherwise be competing for resources in a drought-stressed woodland. Of the birds designated as woodland specialists, many were recorded utilising dry rainforest at some stage; over half the foraging observations made in dry rainforests were of woodland specialists (Coughlan 2000). This suggests a fairly fluid relationship between the bird faunas of the two habitats and little structure to the dry rainforest bird community *per se.* Kikkawa (1993) noted that monsoon rainforests in the north become refugia in the dry season when not only migrants from the south but also sclerophyll habitat birds from the surrounding areas congregate there. Spangled Drongos and Rainbow Bee-eaters are migrants that become rainforest birds in winter. Many migrant insectivores (cuckoos, whistlers, fantails and monarchs) use fragmented forests as stepping-stones in their north-south migration (Kikkawa 1993).

Thus, while dry rainforests in this study appear to have a discrete avifauna, it is primarily made up of wet forest generalists surviving in marginal habitat and species more commonly associated with woodlands using the dry rainforest as a refuge, either seasonally in response to drought and/or fluctuating resources. Queensland's rainfall is highly variable. 'Average' rainfall is rare and variation between years is high (Wilcocks and Young 1991). Under these circumstances it is difficult to differentiate between, or account for, natural variation in bird communities and variations which result from short-term climatic vicissitudes and the resultant variations in resource supply. Severe and prolonged drought may be a feature of the Australian climate which recurs regularly and to which the avifauna have adapted.

Conservation significance of dry rainforest

Although dry rainforest bird communities were distinct in species composition from those of the surrounding woodlands, the dry rainforest community was one of forest generalists, not rainforest specialists. Many studies have shown that forest interior species are adversely affected by habitat fragmentation (Howe *et al.* 1984) and this could explain the absence of rainforest specialists, such as fruit-eating pigeons, which may have been lost over the long-term isolation of the fragments, leaving behind only forest generalists. Dry rainforest patches are probably too small to support rainforest specialists. Conversely, the lack of dry rainforest specialists (in contrast to wet forests) suggests that dry rainforests may not have existed as a distinct vegetation type for long enough to develop a suite of endemic species. Alternatively, dry rainforests might be relatively transient. That the fauna may represent a suite of recent invaders from eucalypt woodlands or wet rainforests is consistent with the view presented by Bowman (2000) that the dry rainforest flora is quite dynamic in the landscape, being able to establish quickly but be easily displaced by fire. This lack of stability of the vegetation type may have precluded the specialisation of its associated avifauna.

A decline in the quality of dry rainforest habitat from the effects of cattle, pigs, weeds and fire, may reduce habitat suitability for birds in several ways. Woodland birds may move into dry rainforest patches as they become degraded and the larger territorial species may be successful in excluding dry rainforest species. Habitat may simply become unsuitable for many dry rainforest birds. Dry rainforest at Fanning River, for example, is more open and fragmented and shows a greater influence of woodland species in the dry rainforest and a less discrete dry rainforest avifauna.

Dry rainforest patches support a distinct avifauna that, if lost, will reduce regional bird diversity by at least thirteen species. Dry rainforest patches also provide an important set of supplementary resources for woodland birds. This study was conducted entirely during a severe drought, so it is not known to what extent the woodland avifauna might utilise dry rainforest resources at other times. It is also noted that the small habitat islands studied here were of sufficient size to support a discrete, functional bird assemblage and provide habitat for seasonal and

latitudinal migrants, as well as supplementary habitat for woodland birds. Since most rainforest birds are protected in national parks within their range (Kikkawa 1993, and given the low densities of forest birds in dry rainforest and the relatively small area of dry rainforest habitat in the landscape, dry rainforest is probably not crucial for the survival of rainforest birds. This does not mean that dry rainforest does not have an important role in the landscape. Keystone resources provided by dry rainforest may be important in times of scarcity in woodlands such as during drought or after fire, particularly as dry rainforests tend to grow in fire protected locations.

Many rainforest bird species are averse to crossing even short barriers (Howe *et al.* 1981), so it would be of some interest to examine bird populations in dry rainforest patches to see how isolated they really are. It is likely that there will be a spectrum of levels of contact with other patches, depending on the distance between patches and the nature of the intervening matrix. Genetic studies in the Northern Territory have shown that relatively frequent gene flow between plant populations is mediated by mobile frugivores (Shapcott 1999). Studies on flightless insects may give some insights into historical distribution of dry rainforest vegetation, particularly considering their limited dispersal capabilities and specialisation to microhabitats (Kahn and Lawrie 1987, Solem and McKenzie 1991).

The interaction between frugivores and the plant species that they disperse is an integral component of the dry rainforest-savanna woodland system (Woinarski *et al.* 1992, Shapcott 1999). Although dry rainforest supported many frugivorous birds in this study, it is not known what percentage were fruit predators (feeding on fruit pulp without performing dispersal) and active seed dispersers (Herrera 1998). Nevertheless, the rainforest habitat is probably dependent on frugivorous birds and flying-foxes for seed dispersal. Similarly, the frugivorous forest generalists are dependent on the survival of these remnant patches for their persistence in the northern Australian savanna.

Conservation and management of dry rainforest

Degradation of dry rainforest in northern Queensland is occurring through the invasion of weeds, the influence of feral animals and the intrusion of fires (Fensham 1996). Cattle and pigs destroy understorey vegetation, which allows the infiltration of weed species that alter both the structural and floristic diversity of the understorey. This drastically alters the suitability of the habitat for ground-dwelling birds such as the Australian Brush-turkey. No introduced bird species were recorded but it is not known how many species have disappeared from these forests as a result of habitat degradation caused by cattle, weed invasion and fire. Undoubtedly the damage caused to understorey habitats by cattle and pigs has had an adverse influence on ground-dwelling birds in both dry rainforest and woodlands. Few studies have examined the effects of grazing on birds but declines in such species as finches and the Purple-crowned Fairy-wren have been linked to habitat alteration as a result of grazing (Woinarski 1993a). Control of grazing in dry rainforest patches may be crucial if they are to avoid further degradation.

The maintenance of floristic diversity and viability of dry rainforest patches is dependent on populations of animals, particularly birds, which migrate between them. Conversely, some forest birds may be dependent on a network of patches to provide all their resource needs (Recher and Holmes 1985, Price *et al.* 1999). However, the more degraded the patches become, the less likely they are to support populations of forest birds. In southern Queensland, aggressive territorial species, such as the Noisy Miner and the Australian Magpie, have become keystone competitors, excluding small insectivores from forest remnants (Catterall *et al.* 1997). The degradation of dry rainforest vegetation, as well as the reduction in the number of patches in a region through clearing, could cause a decline in abundance of forest birds and the eventual demise of the network of dry rainforest patches. More studies are needed that assess, over a range of dry rainforest types, the relative roles of forest and woodland birds in dispersal of dry rainforest seeds and the movements between patches. Such studies in the northern Territory dry rainforest estate have been extremely useful in identifying priorities for conservation based on individual species' foraging needs and preferences (Price *et al.* 1996, 1999).

The dry rainforests in Queensland present a complex conservation problem because most patches occur on large leasehold grazing properties and in small, scattered isolates, making acquisition for reserves unrealistic. The majority of rainforests in Queensland National Parks estate are wetter coastal rainforests. Dry, seasonal forest types are less protected. In any case, National Park status does not necessarily afford protection to forest patches, as demonstrated by Forty Mile Scrub National Park, a large proportion of which is infested with Lantana (Fensham *et al.* 1994) and is at great risk from the fires fuelled by its growth (Fensham 1996b). Thus, the effective conservation of dry rainforests in Queensland might only be achieved through active management of remaining patches, with the cooperation of landholders. As is the case for other habitats not represented in reserves, there is a pressing need for policies and resources for off-reserve management if this important and novel forest type and its avifauna is to be conserved.

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