

- Burger, J. & Gochfeld, M. 1981. Colony and habitat selection of six Kelp Gull *Larus dominicanus* colonies in South Africa. *Ibis* 123, 298-310.
- Coulson G M, & Coulson, R.I. 1982. The significance of rubbish tips as an additional food source for the Kelp Gull and the Pacific Gull in Tasmania. M.Env. Thesis, University of Tasmania, Hobart.
- Everitt, B.S. 1977. *The Analysis of Contingency Tables*. Chapman & Hall, London.
- Fleming, A. 1987. Pacific Gulls inland. *Australian Bird Watcher* 12, 102.
- Fordham, R.A. 1964. Breeding biology of the Southern Black-backed Gull, II: incubation and the chick stage. *Notornis* 11, 110-126.
- Fordham, R.A. 1970. Mortality and population change of dominican gulls in Wellington, New Zealand. *Journal of Animal Ecology* 39, 13-27.
- Greene, H.W. & Jaksic, F.M. 1983. Food-niche relationships among sympatric predators: effects of level of prey identification. *Oikos* 40, 151-154.
- Hockey, P.A.R. 1988. Kelp Gulls *Larus dominicanus* as predators in kelp *Macrocystis pyrifera* beds. *Oecologia* 76, 155-157.
- Hockey, P.A.R. & Bosman, A.L. 1988. Stabilizing processes in bird-prey interactions on rocky shores. Pp. 297-315 in *Behavioral Adaption to Intertidal Life*. Eds G. Chelazzi & M. Vannini. Plenum, New York.
- Hockey, P.A.R., Ryan, P.G. & Bosman, A.L. 1989. Age-related intraspecific kleptoparasitism and foraging success of Kelp Gulls *Larus dominicanus*. *Ardea* 77, 205-210.
- Jones, W.G. 1979. Bird observations, 1979 — Systematic list. *Tasmanian Bird Report* No. 9, 23-43.
- McLachlan, A., Wooldridge, T. & Schramm, M.K.M. 1980. Seasonal abundance, biomass and feeding of shore birds on sandy beaches in the Eastern Cape, South Africa. *Ostrich* 51, 44-52.
- Merilees, W. 1984. Some notes on the foods of the Dominican Gull at Macquarie Island. *Tasmanian Naturalist* No. 79, 5-6.
- Morant, P.D. & Winter, C. 1983. Carrion feeding by Kelp Gulls *Larus dominicanus* in Patagonia, Argentina. *Cor-morant* 11, 65-67.
- Murphy, R.C. 1936. *Oceanic Birds of South America*, Vol. II. American Museum of Natural History, New York.
- Oliver, W.R.B. 1974. *New Zealand Birds*. Reed, Wellington.
- Parmelee, D., Fraser, W. & Glass, B.N.D. 1977. Ecological and behavioural adaptations to Antarctic environments. *Antarctic Journal of the United States* 12 (4), 17.
- Pianka, E.R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences* 71, 2141-2145.
- Serventy, D.L., Serventy, V. & Warham, J. 1971. *The Handbook of Australian Seabirds*. Reed, Sydney.
- Sutton J, 1935. *Gabianus pacificus*, Pacific Gull. *The South Australian Ornithologist* 13, 54-56.
- Thomas, D.G. 1976. Systematic list for 1976. *Tasmanian Bird Report* 6, 2-31.
- Watson, I.M. 1955. Some species seen at the Laverton Salt-works, Victoria, 1950-1953, with notes on seasonal changes. *Emu* 55, 224-248.
- Watson, G.E. 1975. *Birds of the Antarctic and Sub-Antarctic*. American Geophysical Union, Washington.
- Wheeler, W.R. 1946. Pacific Gulls and mussels. *Emu* 45, 307.

The Importance of *Pandanus spiralis* to Birds

Nicolaas A.M. Verbeek¹, Richard W. Braithwaite² and Rosalinda Boasson¹

¹ Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

² CSIRO Division of Wildlife and Ecology, Tropical Ecosystems Research Centre, Private Bag 44, Winnellie N.T. 0821.

EMU Vol. 93, 53-58, 1993. Received 11-12-1991, accepted 25-3-1992

Pandanus spiralis (hereafter referred to as Pandanus) is a conspicuous tree in a variety of habitats in Kakadu National Park. It belongs to a large family (Pandanaeae) of trees, shrubs and climbers of the Old World tropics (Heywood 1978). Its architecture differs from all other trees in the region. The woody stems, 5-8 m high, are covered in tight, spirally arranged, long (1-2

m), narrow (5-7 cm) leaves that are armed with small spines along the margins. Dead, downward hanging leaves may remain on the tree for many years, creating a tough skirt with many potential hiding places for animals. More often the leaves burn off in the frequent fires. Most trees consequently show bare trunks with a

few dead leaves near the top of the trunk below the apical tuft of currently green leaves.

The species often grows in dense stands. Experimental exclosures for water buffalo *Bubalus bubalis* and pigs *Sus scrofa* produce a dense thicket of Pandanus within two years (Braithwaite unpubl.). The two lowland Pandanus species of the Top End, *P. spiralis* and *P. aquaticus*, reach their greatest abundance close to the northern coast. However, when the explorer Ludwig Leichhardt reached the buffalo-affected areas near present-day Oenpelli in August 1845, his frequent references to Pandanus changed from 'belt, grove or thicket' to 'scattered stands or trees' (Leichhardt 1847). Similarly, when Knut Dahl moved north-east from the coastal Daly River area and encountered the expanding distribution of exotic water buffalo and pigs in the Adelaide River area in 1894, he also used the description 'scattered' as a relative term for Pandanus (Dahl 1926). It is clear from the diaries of the anthropologist and zoologist Donald Thomson (Dixon & Huxley 1985) that in the remote and intact parts of eastern Arnhem Land in the 1930s, Pandanus thickets were rich in animals.

That several Australian birds appear to be associated with Pandanus is suggested by the old vernacular names of some bird species, such as the Pandanus Bird, now referred to as the Blue-faced Honeyeater* and the Pandanus Pigeon, now known as the Bar-shouldered Dove (Schodde & Tidemann 1986). The Crimson Finch has a habitat listed by Slater (1974) as 'river and swampy vegetation, particularly Pandanus'. Further, Immelmann (1982, p. 55) wrote 'the Crimson Finch usually constructs its nest on the butts of Pandanus leaves about 3-15 m from the ground'. Similarly, for the Purple-crowned Fairy-wren *Malurus coronatus*, Rowley (1988) described 'their specialized habitat (as) ... the undergrowth of the fringing riverine forest and is of two kinds — thickets of *Pandanus (aquaticus)* or cane-grass ...'. In this study we looked at which bird species showed an affinity for *Pandanus spiralis*, and what the tree had to offer; we investigated how the changes associated with European settlement might have affected these birds.

Methods

To show an affinity for a particular species of tree a bird must be given a choice of different trees. We stud-

ied birds in a gradient of four vegetation types, consisting of pure stands of mixed species of broad-leaved trees, predominantly *Eucalyptus* spp. (see Taylor & Dunlop 1985); stands of roughly four-fifths broad-leaved trees and one-fifth Pandanus; stands of four-fifths Pandanus and one-fifth broad-leaved trees; and pure stands of Pandanus. The first three types of stands were located on the CSIRO Kapalga Field Research Station and the last stand was along the Arnhem Highway at the edge of the flood plain east of the South Alligator River; all are in Kakadu National Park (12°S, 133°E). In each of the four vegetation types we recorded the occurrence of birds in broad-leaved trees and in Pandanus on nine separate days (36 days in all), two consecutive hours per day, between 3 June and 29 July 1989. Observations were made starting about 30 min after sunrise. During each two-hour period we sat in one location and scanned the crowns of a predetermined set of trees every 5 min, which took about 1 min, and recorded all bird species, and the number of each, seen. For each two-hour period we tried to find a different location. Because the birds were not banded, doubtless some were scored more than once. In between scans, we tried to record the behaviour of any bird seen using Pandanus. Aside from these two-hour watches, more than 18 h were spent sitting in, or walking through, more or less pure stands of Pandanus recording any bird seen using this tree and the way it was used.

Fourteen species that were seen less than six times each (in the 72 h of observation) were excluded from the analysis. For the 32 remaining species (Table 1) the data were analysed in two ways.

(1) Only in mixed stand types did the birds have a chance to express a within-stand preference for broad-leaved trees or for Pandanus. In a mixed stand of about four-fifths broad-leaved trees and one-fifth Pandanus, all else being equal, an individual is four times as likely to be sitting in broad-leaved trees as in Pandanus. To give equal weighting, the number of individuals seen in broad-leaved trees was multiplied by one-fifth and those in Pandanus by four-fifths. For example, 17 Brown Honeyeaters in broad-leaved trees and three in Pandanus were transformed to 3.4 and 2.4, respectively, or 41% use of Pandanus by this honeyeater. The same procedure was used to give proper weighting in mixed stands dominated by Pandanus.

(2) Birds using pure stands were assumed to have a choice of being in that stand or to avoid it. In pure stands, the data were directly expressed as a percentage.

* The scientific names for most of these are given in Table 1; where this is not so the scientific name is given at first mention in the text.

Table 1 Numbers of birds from 32 species seen during scans (see Methods) in four types of vegetation: (1) pure stands of broad-leaved trees (E); (2) pure stands of *Pandanus spiralis* (P); (3) mixed stands E > P; and (4) mixed stands P > E.

Species	Vegetation types						Affinity for P (%) ¹	
			3		4		Within types 3 and 4	Between types 1 and 2
	1	2	E	P	E	P		
Peaceful Dove <i>Geopelia placida</i>	1	10	5	0	2	2	13	91
Bar-shouldered Dove <i>Geopelia humeralis</i>	0	0	7	0	19	0	0	—
Red-collared Lorikeet <i>Trichoglossus rubritorquis</i>	0	0	21	0	0	0	0	—
Varied Lorikeet <i>T. versicolor</i>	26	0	56	0	0	0	0	0
Sulphur-crested Cockatoo <i>Cacatua galerita</i>	0	18	0	0	1	10	71	100
Red-winged Parrot <i>Aprosmictus erythropterus</i>	1	0	1	0	14	0	0	0
Northern Rosella <i>Platycercus venustus</i>	5	0	12	0	0	0	0	0
Blue-winged Kookaburra <i>Dacelo leachii</i>	0	6	2	0	6	6	19	100
Forest Kingfisher <i>Halcyon macleayii</i>	0	0	14	0	0	3	18	—
Rainbow Bee-eater <i>Merops ornatus</i>	9	1	0	0	5	0	7	10
Willie Wagtail <i>Rhipidura leucophrys</i>	4	3	10	0	8	14	25	43
Restless Flycatcher <i>Myiagra inquieta</i>	0	4	0	0	2	3	27	100
Lemon-bellied Flycatcher <i>Microeca flavigaster</i>	0	0	5	0	19	2	2	—
Rufous Whistler <i>Pachycephala rufiventris</i>	19	0	5	0	6	1	3	0
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	2	0	2	0	10	2	5	0
White-bellied Cuckoo-shrike <i>Coracina papuensis</i>	7	3	6	0	23	7	7	30
White-winged Triller <i>Lalage tricolor</i>	9	0	0	0	10	0	0	0
Weebill <i>Smicrornis brevirostris</i>	36	0	2	0	0	0	0	0
Red-backed Fairy-wren <i>Malurus melanocephalus</i>	4	0	0	2	5	0	39	0
Black-tailed Treecreeper <i>Climacteris melanura</i>	8	0	9	1	0	0	31	0
Mistletoebird <i>Dicaeum hirundinaceum</i>	5	0	7	0	1	0	0	0

Continued next page

Table 1 Continued.

Species	Vegetation types						Affinity for P (%) ¹	
	1		3		4		Within types 3 and 4	Between types 1 and 2
	E	P	E	P	E	P		
White-throated Honeyeater <i>Melithreptus albogularis</i>	2	0	96	0	6	0	0	0
Brown Honeyeater <i>Lichmera indistincta</i>	9	0	17	3	0	0	41	0
Rufous-banded Honeyeater <i>Conopophila albogularis</i>	0	4	1	0	14	3	5	100
Rufous-throated Honeyeater <i>Conopophila rufogularis</i>	1	0	76	0	1	0	0	0
White-gaped Honeyeater <i>Lichenostomus unicolor</i>	0	0	5	0	11	3	6	—
Blue-faced Honeyeater <i>Entomyzon cyanotis</i>	0	0	3	4	0	6	88	—
Little Friarbird <i>Philemon citreogularis</i>	25	0	70	2	4	0	9	0
Double-barred Finch <i>Taeniopygia guttata</i>	0	6	0	2	0	4	100	100
Crimson Finch <i>Neochmia phaeton</i>	0	14	0	1	0	25	100	100
Long-tailed Finch <i>Poephila acuticauda</i>	7	0	0	5	11	10	39	0
Torresian Crow <i>Corvus orru</i>	0	7	0	0	4	6	24	0

¹ See Methods for how these percentages were obtained.

For instance, seven White-bellied Cuckoo-shrikes in pure broad-leaved stands and three in pure Pandanus were expressed as a 70% preference for broad-leaved trees and 30% for Pandanus.

Results

Habitat preference

In mixed stands, 28 species (Table 1) showed an affinity (59-100%) for broad-leaved trees and only four species had an affinity (71-100%) for Pandanus. In pure stands, six of the 32 species did not occur in either stand, 19 were found only or predominantly (57-100%) in broad-leaved stands and seven were found only or predominantly (91-100%) in Pandanus. However, among these seven, the Peaceful Dove, Blue-winged Kookaburra and Restless Flycatcher appeared to have a strong affin-

ity for broad-leaved trees, judging by their within-habitat choice. Except for these three, those species that showed an affinity for either broad-leaved trees or Pandanus when they had a within-stand choice, tended to maintain this affinity when choosing between pure stands.

The use of Pandanus

Twelve species seen less than five times in Pandanus were excluded from the analysis of how Pandanus was used. In the remaining 17 species, four merely perched in Pandanus, while 13 perched and used the trees as a food source, primarily to glean invertebrates from the leaves (mostly the green leaves) and trunks (Table 2). Only Sulphur-crested Cockatoos ate the fruits (Table 2) and outside of the Pandanus fruiting season (June to October, Brock 1988) the tree would probably be of little interest to them. Of the two finches that showed a

strong affinity for *Pandanus* (Table 1), the Double-barred Finch was never seen to obtain any food from the tree, but the Crimson Finch gleaned many invertebrates from the leaves. However, most of the food of the Crimson Finch and all the food of the Double-barred Finch was obtained on the ground.

Among the many honeyeaters (Table 1 & 2), only Blue-faced Honeyeaters showed a strong affinity for *Pandanus* even when broad-leaved trees were available. In mixed stands they flew from one *Pandanus* to the next, bypassing broad-leaved trees. They searched for food between the leaf bases, going all around the trunk before moving to the next *Pandanus*. If they showed up at all, they would deal with the *Pandanus* under observation in a few minutes and then would not be seen again for the rest of our two-hour stint, suggesting that they probably covered a large area each day in search of *Pandanus*. The other species in Table 2, such as the Torresian Crow and White-bellied Cuckoo-shrike, used *Pandanus* opportunistically. We saw a pair of Torresian Crows digging deep at the bases of the *Pandanus* leaves and snapping at small frogs *Litoria bicolor* (reputedly

an amphibian *Pandanus* specialist) that jumped out of their day-time hiding places.

Incidental observations showed that several species (Crimson Finch and Double-barred Finch regularly, and Little Friarbird on one occasion) fled into *Pandanus* when startled by us or when potential predators appeared (Brown Goshawk *Accipiter fasciatus*, Australian Hobby *Falco cenchroides* and Blue-winged Kookaburra). Southern Boobook *Ninox novaeseelandiae*, Barn Owl *Tyto alba*, Crimson Finch and Double-barred Finch used the skirts of dead leaves to roost in. We also found a pair each of Crimson Finches and Long-tailed Finches nesting among the dead leaves.

Discussion

The number of species interested in *Pandanus* detected by the present study is very low. In a wetland study on Kapalga during the 1980s, G.R. Friend (pers. comm.) also recorded low abundance and diversity of birds in 'Pandanus-lawn' habitat, compared with other habitats.

Table 2 Numbers of birds from 17 species seen perching on *Pandanus spiralis* and where they obtained food in this tree species.

Species	Perch on		Food obtained from			
	Leaves	Trunks	Green leaves	Dead leaves	Trunks	Fruit
Peaceful Dove		16				
Bar-shouldered Dove		8				
Sulphur-crested Cockatoo		14				13
Blue-winged Kookaburra		7				
Willie Wagtail	10	24	6	6	6	
Restless Flycatcher	6	4	3			
Lemon-bellied Flycatcher	8		2		1	
White-bellied Cuckoo-shrike	7	19	10	1	2	
Red-backed Fairy-wren	23	5	14	1		
Rufous-banded Honeyeater	4		9			
White-gaped Honeyeater	1	2	6	1	1	
Blue-faced Honeyeater	8	1	16	8		
Little Friarbird	11	3	2	9	1	
Double-barred Finch	49	2				
Crimson Finch	57	2	14			
Long-tailed Finch	26	2	1	1	1	
Torresian Crow	2	8	7			

A number of bird species probably used *Pandanus* thickets in the past and may have been more abundant than at present, but it seems clear now that any such association would have been facultative rather than obligate. Only four species were shown (Table 1) to have a consistent relationship with *Pandanus*: Sulphur-crested Cockatoos feed on the fleshy endoderm of the proximate end of the fruit and disperse the seeds (Andersen & Braithwaite 1994), Crimson and Double-barred Finches appear to derive protection from the unusual architecture of the *Pandanus* and for Blue-faced Honey-eaters it appears to provide an important food source.

For some species of birds *Pandanus* seems important for nesting, roosting, safety and/or food. These four habitat uses are probably influenced by fire. Although fires are likely to have been frequent in this habitat for millennia (Braithwaite 1991), they have become more intense due to changes in the season of burning (Braithwaite & Estbergs 1985). Nevertheless, other factors also have been influential on *Pandanus* habitat, for instance, water buffalo and pigs eat the leaves, fruit, seedlings and basal suckers. Small enclosure experiments (Braithwaite unpubl. data) showed that even quite a low density of these exotic mammals is sufficient to maintain an open structure where *Pandanus* thickets would otherwise form.

The value of the habitat probably did not derive from the presence of *Pandanus* as such but from the structural consequences of its once high abundance. Some support for the idea that the structure of the thicket was its most important feature is provided by the observation that the marsupial mouse *Sminthopsis virginiae* has become locally abundant in coastal areas where the exotic shrub *Mimosa pigra* simulates native *Pandanus* thickets (Braithwaite & Lonsdale 1987). Although we have no evidence that *Pandanus* thickets were once full of animal life, except for the diaries of Thomson (Dixon & Huxley 1985), we suggest that the disappearance of the dense thickets may well have altered the numbers of individuals and the relative composition of all vertebrate groups that inhabited them. In this study we attempted to trace the ghosts of that past landscape, but the functional significance of it can only be fathomed by experimentally re-establishing the large *Pandanus* thickets that Leichhardt and others saw. The large-scale fencing required for this field experiment is expensive. However, natural resource managers may well come to see 'conservation fencing' as a legitimate,

routine practice in landscape restoration and management.

Acknowledgements

NAMV and RB thank CSIRO Tropical Ecosystems Research Centre at Winnellie for hospitality, and particularly Heather Smith and Darryl Murphy, who greatly facilitated our stay. We thank the Australian National Parks and Wildlife Service for permission to work in Kakadu National Park. We thank Stephen Morton and Richard Noske for their careful reading of the manuscript.

References

- Andersen, A.N. & Braithwaite, R.W. 1994. Plant-animal interactions in the Kakadu region of northern Australia. In: Geobotany of the Alligator Rivers Region. Ed. C.M. Finlayson. Junk, The Hague. In press.
- Braithwaite, R.W. 1991. Aboriginal fire regimes of monsoonal Australia in the 19th century. *Search* 22, 247-249.
- Braithwaite, R.W. & Estbergs, J.A. 1985. Fire patterns and woody vegetation trends in the Alligator Rivers region of northern Australia. Pp. 359-364 in *Ecology and Management of the World's Savannas*. Eds J.C. Tothill & J.J. Mott. Australian Academy of Science, Canberra.
- Braithwaite, R.W. & Lonsdale, W.M. 1987. The rarity of *Sminthopsis virginiae* (Marsupialia: Dasyuridae) in relation to natural and unnatural habitats. *Conservation Biology* 1, 341-343.
- Brock, J. 1988. *Top End Native Plants*. Brock, Winnellie.
- Dahl, K. 1926. In *Savage Australia*. Allan, London.
- Dixon, J.M. & Huxley, L. 1985. *Donald Thomson's Mammals and Fishes of Northern Australia*. Nelson, Melbourne.
- Heywood, V.H. 1978. *Flowering Plants of the World*. Oxford University Press, Oxford.
- Immelmann, K. 1982. *Australian Finches*. Angus & Robertson, Sydney.
- Leichhardt, L. 1847. *Journal of an Overland Expedition in Australia*. Boone, London.
- Rowley, I. 1988. The Purple-crowned Fairy-wren: an RAOU conservation statement. RAOU, Melbourne.
- Schodde, R. & Tidemann, S. 1986. (Eds) *The Reader's Digest Complete Book of Australian Birds*. Reader's Digest, Sydney.
- Slater P. 1974. *A Field Guide to Australian Birds*, Passerines. Rigby, Adelaide.
- Taylor, J.A. & Dunlop, C.R. 1985. Plant communities of the wet-dry tropics of Australia: the Alligator Rivers region, Northern Territory. *Proceedings of the Ecological Society of Australia* 13, 83-127.