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RELATIONSHIPS BETWEEN CONTROL OF WATER REGIMES IN RIVER RED GUM WETLANDS AND ABUNDANCE OF WATERBIRDS

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Twelve wetlands on the floodplain of the Murrumbidgee River (Murray-Darling Basin, Australia) were surveyed for waterbirds while they were flooded during 1989–90. At six of the wetlands, water regimes were controlled slightly or not at all; at the other six sites water regimes were controlled moderately or heavily. Abundances of six species of waterbird were related to control of water regimes at the wetlands during the early, middle and/or late stages of the flood. Little Pied Cormorants, White-faced Herons and ducks favoured wetlands with no or low degrees of water control during the early flood phase. Little Black and Little Pied Cormorants preferred wetlands with medium or heavy control of their water regimes during the late flood stage. Relationships between abundances of waterbirds and areas of wetland habitats varied with flood phase. During the first phase of flooding, abundances of several species of waterbirds were correlated with wetland area; during the second stage a few species were; and during the third stage of flooding, abundances of Pelecaniformes and the Pacific Black Duck were correlated with wetland area. The percentage of all waterbirds that were on the heavily regulated wetlands increased between the middle and late flood phases.

INTRODUCTION

Many wetlands in the Murray-Darling Basin have controlled water regimes (Broome and Jarman 1983; Pressey 1990; Green and Dunkerley 1992; Magrath 1992; Shepheard 1992; Thornton and Briggs 1994). The degree of control of their water regime varies between wetlands (Seddon *et al.* 1997). Some wetlands in the Murray-Darling Basin never dry out, although they did originally (Pressey 1990; Thornton and Briggs 1994; Seddon *et al.* 1997). Effects of controlling water regimes of wetlands on abundances of waterbirds are likely to be twofold. Where it causes permanent flooding of entire wetlands or rapid changes in water level, hydrological control is likely to reduce the value of wetlands as habitat for many waterbirds. This is because permanent inundation and rapid changes in water levels reduce abundances of wetland invertebrates and plants, the food of many waterbirds (Broome and Jarman 1983; Maher and Carpenter 1984; Roberts and Ludwig 1991; Timms 1992; Briggs, Thornton and Lawler unpubl. data). Conversely, wetlands with controlled water regimes, especially if they are permanently inundated, can provide habitat for waterbirds during dry periods when wetlands without controlled water regimes do not contain surface water (Briggs and Lawler 1991; Briggs *et al.* 1993).

The major aim of this study was to investigate whether abundances of waterbirds on wetlands were related to control of wetland water regimes. We also investigated relationships between abundances of waterbirds and wetland or habitat areas, relationships between waterbird numbers and whether the wetland dried completely prior to flooding, and how these relationships varied with stage of flood (early, middle, late).

STUDY SITES

The study sites were 12 wetlands between Wagga Wagga and Hay on the floodplain of the Murrumbidgee River, in southern inland New South Wales, Australia (Fig. 1). They included billabongs (= oxbow lagoons), depressions and flooded creeks (Table 1). The wetlands filled from floods in the Murrumbidgee River, local rainfall, canals, pumping from the river, used irrigation water, or a combination of two or more of these. At sites with controlled water regimes, water was impounded by banks or weirs. Durations of inundation in the wetlands varied from a few months to permanent, and local regulation of their water levels (hydrological control) ranged from none through slight, medium (= moderate), to heavy (= high) (Table 1). Further details of the study sites are given in Briggs *et al.* (1994, 1997).

At six of the study wetlands, water regimes were controlled slightly (2 sites) or not at all (4 sites); at the other six sites water regimes were controlled moderately (3 sites) or heavily (3 sites; Table 1). The wetlands with no hydrological control filled and dried according to river level and rainfall. Sites with slight hydrological control received some used irrigation water or had water impounded by a low bank. These wetlands still dried completely between floods, and their natural hydrology overrode artificial manipulation. Artificial regulation (by pumping or diverting water into or out of the site, and by structures used to retain water) of the water regimes of wetlands with moderate hydrological control overrode their natural hydrology, but they still flooded on high river flows. Water levels were completely controlled by weirs or canals at heavily regulated sites. Further details of control categories are given in Thornton and Briggs (1994) and Briggs *et al.* (1994, 1997). Five wetlands dried completely prior to the survey, and four plus the three heavily controlled sites did not (Table 1).

All the wetlands contained open, treeless areas (inundated permanently, or temporarily during floods) and areas of live River Red Gums *Eucalyptus camaldulensis*. The River Red Gums usually enclosed the open area of wetland. During floods, rising water filled the treeless areas first, and then inundated the River Red Gums. With the exception of Webbs, the moderately and heavily controlled wetlands also contained areas of dead River Red Gums (killed by prolonged inundation). Dead River Red Gums were along the edge of open areas, or in clumps throughout the wetlands. Emergent aquatic plants (mostly *Eleocharis* spp., *Paspalum* sp., and *Vallisneria spiralis* with emergent flowers) were present at Dixons and Talbot, and at the unregulated and slightly regulated wetlands except Wowong.

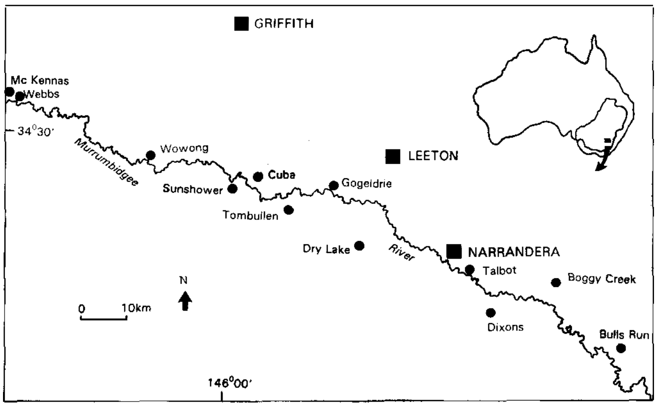

Figure 1. *Locations of study sites.*

TABLE 1

Characteristics of the study wetlands. Area (ha) is maximum inundated area during the study period. Maximum areas of component habitats are given in Briggs *et al.* (1994, 1997). Water control categories are described in Thornton and Briggs (1994) and in Briggs *et al.* (1997).

Wetland	Area	Landform	Degree of water control	Dried prior to study
Bulls Run	168	Depression	None	Yes
Boggy Creek	83	Spreading creek	None	Yes
Dry Lake	410	Depression	None	Yes
Wowong	256	Oxbow lagoon	None	No
Sunshower	177	Oxbow lagoon	Slight	Yes
McKennas	212	Oxbow lagoon	Slight	Yes
Dixons	242	Dammed creek	Medium	No
Cuba	390	Oxbow lagoon	Medium	No
Webbs	139	Oxbow lagoon	Medium	No
Talbot	90	Excavated and dammed creek	Heavy	No[1]
Gogeldrie	88	Depression and oxbow lagoon	Heavy	No[1]
Tombullen	309	Depression	Heavy	No[1]

[1]The heavily controlled wetlands were excluded from the prior drying analyses because they differed from the other permanent sites (see text).

Water levels at most of the wetlands rose as a result of high river flows or rainfall during the early flood phase (Fig. 2). The exceptions were two of the heavily controlled sites, whose water levels fell during the early flood stage (Fig. 2). During the middle flood phase, water levels at the study wetlands started to recede, except at the heavily regulated wetlands where they rose (Fig. 2). The wetlands dried back in the late flood phase, and some sites with no or slight hydrological control dried entirely (Fig. 2).

METHODS

Waterbirds at the study sites were surveyed at approximately six weekly intervals between April 1989 and June 1990 (Fig. 2). Water levels were recorded at some sites in February 1989 prior to the commencement of the surveys (Fig. 2). Surveys at Dixons, Webbs and Dry Lake commenced in May 1989, and at Boggy Creek in August 1989. Waterbirds were surveyed by boat, canoe, wading and walking. At each site at least 50 per cent, and usually more than 90 per cent, of the areas of open water, live River Red Gums, dead River Red Gums and emergent aquatic plants were surveyed. Partial counts of waterbirds within these habitats were extrapolated on the basis of habitat area to give complete counts for each site.

Numbers of waterbirds at the wetlands, areas of the wetlands and areas of their component habitats were averaged between the three surveys carried out in each of the early, middle and late stages of the flood. The component habitats were areas of: open water; flooded live River Red Gums; flooded dead River Red Gums; and emergent aquatic plants. The early flood phase comprised counts in April, May, and June/July 1989 (survey trips 1, 2 and 3). The middle flood phase comprised counts in August, September/October and November 1989 (survey trips 4, 5 and 6). The late flood phase comprised counts in February, April and June 1990 (survey trips 7, 8 and 9). Mean numbers of waterbirds at a wetland, and mean areas of the wetlands and of their habitats during the early, middle and late flood stages were used in the analyses.

Dry sites and sites which were not surveyed early in the study were treated as missing data. Sunshower was dry during survey trip 7; Dry Lake, Sunshower and McKennas were dry during survey trip 8; and Dry Lake remained dry for survey trip 9. A small increase in flow in the Murrumbidgee River towards the end of the study period reflooded Sunshower and McKennas between survey trips 8 and 9 (Fig. 2). Not all species of waterbird were present at sufficient sites to be analysed in each flood stage. Species that were present at six or more sites, during at least one of the three surveys in a flood stage, were included in the analyses for that phase (Appendix 1). Appendix 1 shows the flood phases when each species was present at sufficient sites for analysis.

We investigated effects of control of wetland water regime (= hydrological control; presence and degree), prior drying, habitat and wetland areas (mean areas of open water, flooded live River Red Gums, dead River Red Gums, emergent aquatic plants, and area of flooded wetland) on abundance of waterbirds in the three flood stages by simple linear regression. We used dummy variables for presence (1, none + slight; 2, medium + heavy) and degree (1, none; 2, slight; 3, medium; 4, heavy) of hydrological control, and for presence of prior wetland drying (1, no prior drying; 2, prior drying). Areas of total wetland, open water, live River Red Gum, dead River Red Gum and of emergent aquatic plants were estimated on each field trip by marking their extent onto aerial photographs. Numbers of waterbirds were transformed by log $(x + 1)$ prior to analysis to ensure that their variances were independent of their means, and to normalize the data.

During the first and last flood phases there were very large numbers of Great Cormorants *Phalacrocorax carbo* at one site, Tombullen, because they were nesting there (e.g. 1 800 nests on survey trip 2). We consequently analysed some of the data excluding Great Cormorants at Tombullen. The highly regulated wetlands, Talbot, Gogeldrie and Tombullen, were excluded from the analyses of effects of prior drying on waterbird abundance. These sites were permanently inundated, but their water levels varied rapidly and at irregular intervals. They were very different from the other permanently inundated wetlands, where water levels rose and fell evenly with floods even though they retained a permanent pool of water in their central basins.

RESULTS

Six species of waterbird out of the 21 tested showed relationships with hydrological control in at least one flood stage. Relationships were negative during the early and middle flood phases, and positive during the last phase (Table 2). Ducks, in particular, favoured wetlands without water control during early flooding. In contrast, Little Black Cormorants *P. sulcirostris* and Little Pied Cormorants *P. melanoleucos* preferred controlled wetlands during late flooding. During the early flood stage, Australian White Ibis *Threskiornis*

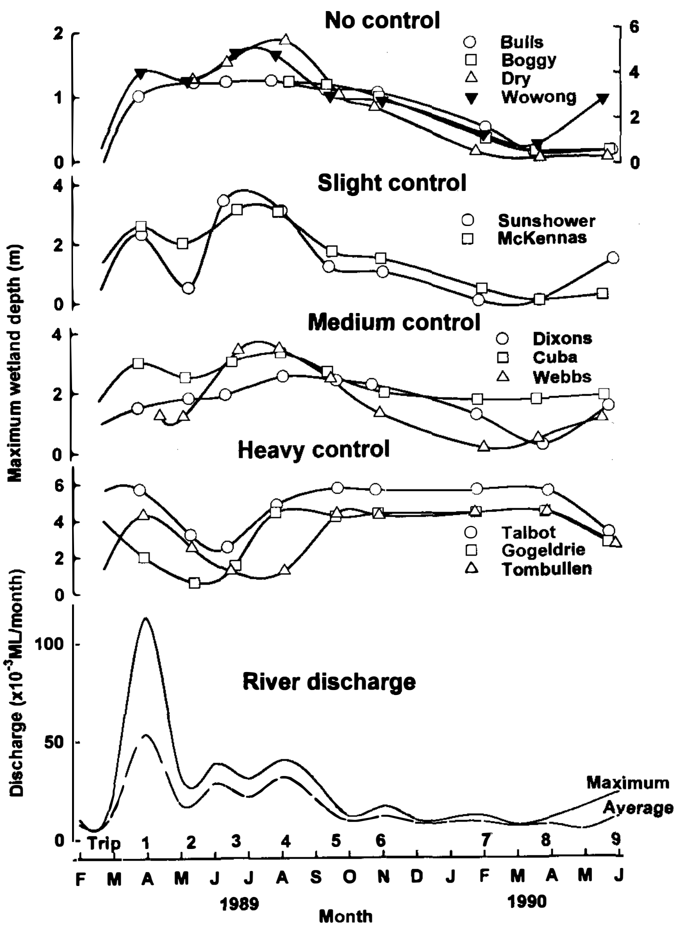

Figure 2. *Dates of survey trips plotted on smoothed water levels at the study wetlands; the top right hand axis applies to Wowong. Maximum wetland depth is the depth of water at the deepest part of each wetland. Narrandera is the gauging station for river discharge. Survey trips 1, 2 and 3 comprised the early flood stage, trips 4, 5 and 6 the middle, and trips 7, 8 and 9 the late flood stage. Water levels at some sites were recorded in February 1989, but waterbirds were not surveyed. Redrawn from Briggs* et al. *(1997).*

molucca, Pacific Black Duck *Anas superciliosa* and Chestnut Teal *A. castanea* were more abundant on wetlands which had dried prior to the study than on wetlands that retained water (regression, all $P < 0.05$). No species showed a relationship with prior drying during the middle period of flooding. During the late flood period, there were more Little Black Cormorants and Australian Wood Ducks *Chenonetta jubata* on wetlands which did not dry before the study than on wetlands which had dried before reflooding (regression, both $P < 0.01$).

The average areas of inundated wetlands with uncontrolled and with slightly, moderately and heavily controlled water regimes altered during the study period (Fig. 3). Markedly smaller areas of wetlands with uncontrolled and slightly controlled water regimes were inundated in the late flood stage compared with the earlier two stages (Fig. 3). The mean area of moderately controlled wetlands that was inundated decreased between the middle and late flood periods, whereas the mean area of heavily controlled wetlands that was inundated increased between the early and middle flood periods (Fig. 3). Across the 12 study sites the proportion of heavily controlled wetland area that was inundated increased during the study; the proportion of moderately controlled wetland that was inundated remained the same; and the proportion of slightly controlled or unregulated wetland that was inundated decreased with time. In the first flood phase, wetlands in the heavily regulated category comprised 18 per cent of the total area of flooded wetland. This figure trebled to 57 per cent in the last flood phase. In contrast, inundated wetland that was not hydrologically controlled comprised 38 per cent of the total area of flooded wetland in the first flood phase, but only 10 per cent of the total area of flooded wetland in the last flood phase.

Excluding Great Cormorants at Tombullen, numbers of waterbirds on the heavily regulated wetlands increased between the middle and late flood stages,

TABLE 2

Relationships between presence and degree of hydrological control and abundance of waterbirds at the study sites during the early, middle and late flood stages. Only significant relationships (regression, $P \leq 0.05$) are shown. ns, no significant relationship; –ve, negative relationship; +ve, positive relationship with hydrological control. Significances of regression relationships are given in Appendix 2.

	Flood stage					
	Early		Middle		Late	
Species	Presence[A]	Degree[B]	Presence[A]	Degree[B]	Presence[A]	Degree[B]
Little Black Cormorant	ns	ns	ns	ns	+ve	+ve
Little Pied Cormorant	ns	–ve	ns	–ve	+ve	+ve
White-faced Heron	–ve	ns	ns	ns	ns	ns
Pacific Black Duck	–ve	–ve	ns	ns	ns	ns
Grey Teal	–ve	–ve	–ve	–ve	ns	ns
Chestnut Teal	ns	–ve	ns	–ve	ns	ns
All waterbirds	ns	ns	ns	–ve	ns	ns

[A]Presence of hydrological control indexed as 1, none plus slight; 2, medium plus heavy.
[B]Degree of hydrological control indexed as 1, none; 2, slight; 3, medium; 4, heavy.

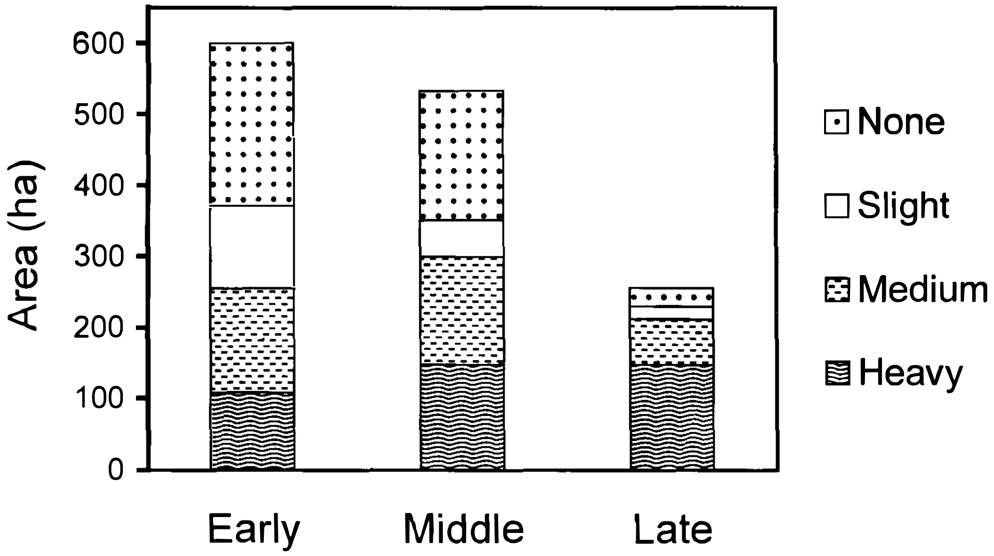

Figure 3. *Mean areas of inundated wetland by category of hydrological control during the early, middle and late flood stages.*

whereas on the slightly and unregulated wetlands numbers fell (Fig. 4). The percentages of waterbirds on the heavily controlled sites during the early, middle and late flood stages were respectively 10 per cent, 11 per cent and 32 per cent. Excluding Great Cormorants at Tombullen, numbers of waterbirds (means of three survey trips within each flood phase) at the study sites were 5 593, 6 105 and 4 853 respectively during the three consecutive flood phases (Table 3). (Boggy Creek was excluded from this analysis because it was not surveyed during the first flood stage). Most of the overall fall in numbers between the middle and late flood phases resulted from a fall in the total numbers of Grey Teal *A. gracilis* at the study sites (from 2 540 to 1 181 birds). Numbers of some other species at the study sites, particularly White-faced Herons *Egretta novaehollandiae*, Royal Spoonbills *Platalea regia* and Pacific Black Ducks, increased between the middle and late flood periods. Even though numbers of waterbirds (excluding Great Cormorants at Tombullen) increased between the middle and late flood phase at the heavily regulated wetlands (Fig. 4), densities of waterbirds at these wetlands remained lower than on the less controlled wetlands in the same flood phase (Table 4).

With Great Cormorants at Tombullen included, some trends were different (Tables 3, 4). The percentage of all waterbirds on the heavily controlled wetlands during the first flood phase was 33 per cent, with 11 per cent during the middle phase and 41 per cent during the late flood phase. Including Great Cormorants at Tombullen and excluding waterbirds at Boggy Creek, numbers of waterbirds (means of three

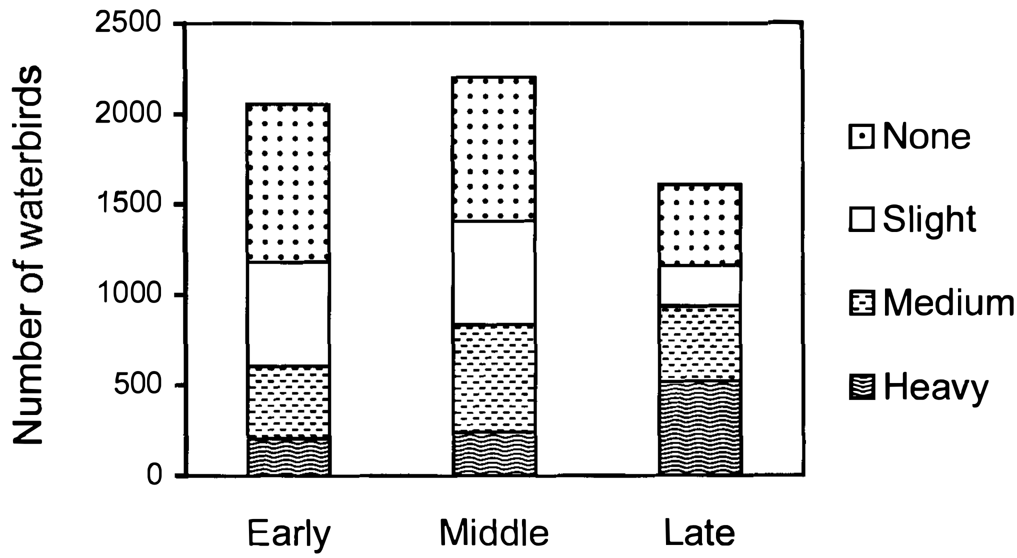

Figure 4. *Mean number of waterbirds per wetland by category of hydrological control during the early, middle and late flood stages. Great Cormorant at Tombullen are excluded.*

TABLE 3

Numbers of Pelecaniformes (P), Pelecaniformes excluding Great Cormorant *P. carbo* at all sites (P-GC), Ciconiiformes (C), Anatidae (A), Anatidae excluding Grey Teal *A. gracilis* (A-GT) and Rallidae plus Podicipedidae (R+P) at the study sites during the early, middle and late flood stages. Numbers are means of the three trips within the flood stage summed across all sites. Numbers of waterbirds at Boggy Creek are excluded because this site was not surveyed during the early flood stage. Figures in parentheses are numbers of Pelecaniformes excluding numbers of Great Cormorant at Tombullen only.

Flood stage	P	P-GC	C	A	A-GT	R+P
Early	2 859	618 (743)	501	4 286	1 685	63
Middle	1 060	917 (1 038)	506	4 426	1 888	135
Late	1 004	309 (335)	1 042	3 351	2 170	125

TABLE 4

Mean densities ± s.e.(n) (birds ha^{-1}) of waterbirds on the study wetlands with no, slightly, moderately and heavily controlled water regimes during the early, middle and late flood stages. The density of waterbirds on 0.6 ha of flooded wetland at McKennas in the late flood stage (470 waterbirds ha^{-1}) is excluded from the data.

Control category	Flood stage Early	Middle	Late
None	4.0 ± 0.7 (3)	5.8 ± 1.8 (4)	23.0 ± 11.0 (4)
Slight	4.8 ± 1.3 (2)	5.8 ± 1.5 (2)	4.6 (1)
Medium	3.0 ± 0.5 (3)	3.8 ± 0.3 (3)	5.9 ± 0.9 (3)
Heavy[1]	1.7 ± 0.4 (3)	2.0 ± 0.8 (3)	3.7 ± 0.9 (3)
Heavy[2]	5.0 ± 3.7 (3)	2.0 ± 0.8 (3)	4.4 ± 1.0 (3)

[1]Excluding Great Cormorant *P. carbo* at Tombullen.
[2]Including Great Cormorant at Tombullen.

survey trips) at the study sites in the consecutive flood phases were 7 709, 6 127 and 5 522 (Table 3). Average numbers of Great Cormorants at Tombullen during the first flood phase were 2 116, only 22 during the middle phase, and 669 during the late phase. The mean numbers of Great Cormorants at Tombullen during the early and late flood stages were an order of magnitude higher than their numbers at the other sites. At the other sites combined, the mean numbers of Great Cormorants during the three flood phases were 124, 124 and 27.

The area of dead River Red Gums was positively correlated with degree and presence of hydrological control during all three flood phases (regression analyses, all $P \leq 0.05$). The area of live River Red Gums was negatively related to degree of water control during the first flood phase. During the middle flood phase, the area of aquatic plants was negatively related to degree of water control. During the last flood phase, wetland area was positively related to degree of water control (regression analyses, all $P \leq 0.05$). There were no other relationships between areas of wetland or of wetland habitats and degree or presence of hydrological control. There were no relationships between wetland or habitat areas and whether the wetland had dried completely prior to the flood period.

Relationships between abundances of waterbirds and areas of wetland and of wetland habitats varied with flood phase. During the first phase of flooding, abundances of several species of waterbirds were correlated with wetland area; during the second stage a few species were; and during the third stage numbers of Pelecaniformes and Pacific Black Ducks were correlated with wetland area. (Table 5). Numbers of Australian Pelicans *Pelecanus conspicillatus*, Little Pied Cormorants, White-faced Herons and Pacific Black Ducks were related to area of open water during the early flood phase; the Intermediate Egret *Ardea intermedia* showed this relationship during the second flood phase; and members of the Pelecaniformes (except the Little Pied Cormorant) showed this relationship during the late flood phase (Table 5).

Most relationships between numbers of waterbirds and area of emergent aquatic plants occurred during the early and middle flood phases (Table 5). The Australian White Ibis was associated with the area of emergent aquatic plants during all three flood stages (Table 5). Abundance of the Yellow-billed Spoonbill *P. flavipes* was related to the area of live River Red Gums during the early and middle flood phase; other species showed relationships only during one flood phase (Table 5). Grey Teal numbers were correlated with the area of live River Red Gums during the early flood phase, whereas Pacific Black Ducks and Australian Wood Ducks showed this relationship during the late stage of flooding. There were significant relationships between abundances of Darters *Anhinga melanogaster*, cormorants and Pacific Black Ducks and area of dead River Red Gums during the late flood stage (Table 5).

DISCUSSION

During the early stage of flooding, the wetlands with less hydrological control provided significantly better habitat for White-faced Herons and Little Pied Cormorants than the wetlands with more hydrological control. Less controlled wetlands provided better habitat for ducks during both the early and middle flood stages. Conversely, the wetlands with more controlled water regimes provided better habitat for Little Black and Little Pied Cormorants during the late flood stage. The degree of water control at a wetland appeared to have a direct effect on the abundance of these waterbirds, rather than waterbird abundance being related to areas of wetland or of wetland habitat, and only indirectly to water control. Wetland area, and the area of dead River Red Gums were both related to degree of hydrological control. Numbers of several species, including the Little Black and Little Pied Cormorant, were correlated with wetland area and/or area of dead River Red Gums in the last flood period. However, except for the Little Black and Little Pied Cormorant, numbers of these species (Australian Pelican, Darter, Great Cormorant, Pacific Black Duck) were not related to degree or presence of water control during the last flood period.

TABLE 5

Relationships between abundance of waterbirds and areas of wetland and of wetland habitats during the early, middle and late flood stages. Only significant relationships (regression, $P \leq 0.05$) are shown. WA, wetland area; OW area of open water; LG, area of live River Red Gum *Eucalyptus camaldulensis*; DG, area of dead River Red Gum; AP, area of emergent aquatic plants; ns, no significant relationship. All relationships were positive. Significances of regression relationships are given in Appendix 2.

Species	Flood stage Early	Middle	Late
Australian Pelican *Pelecanus conspicillatus*	WA, OW	ns	WA, OW
Darter *Anhinga melanogaster*	ns	WA	WA, OW, DG
Great Cormorant *Phalacrocorax carbo*	WA	ns	WA, OW, DG
Little Black Cormorant *P. sulcirostris*	ns	ns	WA, OW, DG
Little Pied Cormorant *P. melanoleucos*	WA, OW, AP	LG	WA, DG
Pacific Heron *Ardea pacifica*	ns	WA	ns
White-faced Heron *A. novaehollandiae*	WA, OW, AP	LG	ns
Great Egret *Egretta alba*	WA, AP	ns	ns
Intermediate Egret *E. intermedia*	ns	WA, OW	ns
Australian White Ibis *Threskiornis molucca*	AP	AP	AP
Straw-necked Ibis *T. spinicollis*	WA, LG	ns	ns
Yellow-billed Spoonbill *Platalea flavipes*	WA, LG	LG	ns
Black Swan *Cygnus atratus*	ns	AP	ns
Pacific Black Duck *Anas superciliosa*	WA, OW, AP	ns	WA, LG, DG
Grey Teal *A. gracilis*	LG	AP	ns
Chestnut Teal *A. castanea*	AP	ns	ns
Australian Wood Duck *Chenonetta jubata*	ns	ns	LG
All waterbirds	WA, OW	ns	WA, OW, DG

The negative relationships between wetlands with controlled water regimes and White-faced Herons, Pacific Black Ducks and Chestnut Teal were also unlikely to be caused by confounding relationships between hydrological control and area of wetland or of wetland habitat. Areas of wetland and of wetland habitats that correlated with abundance of these species were not correlated with presence or degree of hydrological control in the same flood period. Conversely, Grey Teal may have responded positively to the area of live River Red Gums in the first flood phase, and possibly to the area of emergent aquatic plants in the second phase, rather than directly to the degree of water control. The area of live River Red Gums and the degree of water control were inversely related during the first flood phase, as were the area of aquatic plants and degree of water control during the second phase. In a study in the same area, the number of broods of Grey Teal was positively related to the area of live River Red Gum (Briggs *et al.* 1997).

During the last flood stage, Darters, cormorants and Pacific Black Ducks were more abundant on wetlands with more dead River Red Gum. Such wetlands retained water permanently or near-permanently. It is likely that these species of waterbird were responding to the continuing presence of water at the wetlands with dead River Red Gum, rather than to the area of dead trees *per se*.

During the first flood phase, Pacific Black Ducks, Chestnut Teal and Australian White Ibis preferred wetlands which had dried before the study. Presumably, such conditions provide the best food resources for these species (see Maher and Carpenter 1984; Briggs 1988). Wetlands which had not dried entirely before the study were favoured by Little Black Cormorants and Australian Wood Ducks, during the late flood stage. Little Black Cormorants feed mostly on fish (Marchant and Higgins 1990). Wetlands which retained water between floods would be likely to contain more fish than wetlands that dried. Australian Wood Ducks preferred regulated wetlands or narrow, deep oxbow lagoons, that did not dry out. The edges of these permanent wetlands provided the short green herbage favoured by Australian Wood Ducks as food (Kingsford 1989; Marchant and Higgins 1990), while their permanent water provided refuge from predators.

Many species of waterbirds were more abundant on larger wetlands, and on wetlands with larger areas of open water. This tendency was particularly noticeable among the Pelecaniformes during the late flood stage. In a broad-scale survey Kingsford *et al.* (1996) found that numbers of waterbirds were related to wetland area. Wetlands with small areas of open water during the late flood phase were shallow. Darters, Great and Little Black Cormorants and Australian Pelicans would have had difficulty fishing in them (see Marchant and Higgins 1990). The Little Pied Cormorant, the only species of Pelecaniformes whose numbers were not related to the area of open water during the late flood phase, and whose numbers were related to the area of emergent aquatic plants in the first flood phase, is able to use vegetated wetlands and smaller areas of open water than other Pelecaniformes (Marchant and Higgins 1990).

The area of live River Red Gum was an important determinant of numbers of Little Pied Cormorants, White-faced Herons, Straw-necked Ibis *T. spinicollis*, Yellow-billed Spoonbills, Pacific Black Ducks, Grey Teal and Australian Wood Ducks, although the relationships varied with phase of flooding. These species of waterbirds nested in live River Red Gums during the early and middle flood stages in this study (Briggs *et al.* 1994, 1997). The associations between the numbers of Little Pied Cormorants, White-faced Herons, Yellow-billed Spoonbills and Grey Teal and the area of live River Red Gum are likely to reflect the birds' use of live River Red Gums as nesting sites. Numbers of nests or broods of Little Pied Cormorants, White-faced Herons, Yellow-billed Spoonbills and Grey Teal at the study sites were related to the area of live River Red Gums, or to the area of flooded live River Red Gum (Briggs *et al.* 1997). The relationships between areas of live River Red Gums and abundances of Pacific Black and Australian Wood Ducks appeared to reflect habitat preference of non-breeding birds, rather than breeding relationships, because the associations occurred during the late flood phase when nesting had finished.

The highly controlled wetlands held relatively more waterbirds during the last flood phase, when the unregulated or slightly regulated wetlands were small and shallow, or dry. However, densities of waterbirds on the highly controlled sites (excluding the Great Cormorant at Tombullen) were lower than densities on less controlled sites during the same flood period. Highly controlled wetlands where water levels fluctuate rapidly, unpredictably and at short intervals have low numbers of aquatic plants and invertebrates (Broome and Jarman 1983; Wetzel 1990; Bayley 1991; Timms 1992; Briggs, Thornton and Lawler, unpubl. data). They are generally unattractive to waterbirds, compared with wetlands where water levels rise and fall more slowly and evenly.

The marked reduction in numbers of Grey Teal between the middle and late flood phases is in keeping with this species' mobility. Working in the 1950s in the same study area as ours, Frith (1959) noted that Pacific Black Ducks concentrated on remaining water during dry periods, whereas Grey Teal moved out of the area.

Average densities of all waterbirds at the Murrumbidgee study sites were similar or higher than densities in the Paroo wetlands reported by Maher (1991) and Maher and Braithwaite (1992), but lower than the densities of waterbirds in the Namoi wetlands recorded by Broome and Jarman (1983). As Maher (1991) found, densities tended to be high during late flooding (the drying phase), when inundated wetlands were small in area and few in number.

Relationships between hydrological control of wetlands and abundance of individual species of waterbird depended on the stage of the flood cycle. In this study, the habitat value of wetlands for four of the 21 species of waterbirds which could be tested was reduced by hydrological control; in one species there were both positive and negative effects depending on the stage of the flood; and one species benefited overall from hydrological control. Wetlands whose water regimes are heavily regulated provide useful habitat for waterbirds during dry periods (see also Briggs and Lawler 1991; Bancroft *et al.* 1992; Briggs *et al.* 1993), but substandard breeding and feeding habitat for most species of waterbirds at other times (Broome and Jarman 1983; Briggs *et al.* 1995, 1997). Conversely, wetlands with moderate control of their water regimes provide valuable breeding habitat for several species of Pelecaniformes and Ciconiiformes (Briggs *et al.* 1997).

Numbers of most species of waterbirds were not directly affected by hydrological control. Instead, their abundance at a site was related to other habitat factors such as area of the wetland or of one of its component habitats. Control of water regime is one factor in wetland environments; its impacts on waterbirds will be modified by other aspects of wetland environments such as availability of dead and live trees as nest sites (also see Briggs and Thornton 1995; Briggs *et al.* 1995). Nonetheless, presence, degree and type of water control at wetlands affect abundance and breeding of waterbirds (see Broome and Jarman 1983; Kingsford 1994; Briggs *et al.* 1994, 1997, but see Kingsford *et al.* 1996). Degree and type of hydrological control should be recorded routinely in wetland and waterbird surveys, and included as potential explanatory variables in analyses of waterbird abundance and breeding (Briggs *et al.* 1997) at different wetlands.

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APPENDIX 1

Species of waterbirds at the study sites. E, M, L; present at sufficient sites (≥6) for analysis during the early (E), middle (M), late (L) flood stages. Species without E, M or L after their common name were not present at sufficient sites in any flood stage to be analysed individually.

Common name	Scientific name
Great Crested Grebe	*Podiceps cristatus*
Hoary Headed Grebe	*Poliocephalus poliocephalus*
Australasian Grebe	*Tachybaptus novaehollandiae*
Australian Pelican E, M, L	*Pelecanus conspicillatus*
Darter E, M, L	*Anhinga melanogaster*
Great Cormorant E, M, L	*Phalacrocorax carbo*
Pied Cormorant	*Phalacrocorax varius*
Little Black Cormorant E, M, L	*Phalacrocorax sulcirostris*
Little Pied Cormorant E, M, L	*Phalacrocorax melanoleucos*
Pacific Heron M, L	*Ardea pacifica*
White-faced Heron E, M, L	*Ardea novaehollandiae*
Great Egret L	*Egretta alba*
Little Egret	*Egretta garzetta*
Intermediate Egret M, L	*Egretta intermedia*
Rufous Night Heron	*Nycticorax caledonicus*
Glossy Ibis	*Plegadis falcinellus*
Australian White Ibis E, M, L	*Threskiornis molucca*
Straw-necked Ibis E	*Threskiornis spinicollis*
Royal Spoonbill L	*Platalea regia*
Yellow-billed Spoonbill E, M, L	*Platalea flavipes*
Black Swan M, L	*Cygnus atratus*
Australian Shelduck	*Tadorna tadornoides*
Pacific Black Duck E, M, L	*Anas superciliosa*
Grey Teal E, M, L	*Anas gracilis*
Chestnut Teal E, M, L	*Anas castanea*
Australasian Shoveler	*Anas rhynchotis*
Pink-eared Duck	*Malacorhynchus membranaceus*
Hardhead	*Aythya australis*
Australian Wood Duck E, M, L	*Chenonetta jubata*
Musk Duck	*Biziura lobata*
Dusky Moorhen E, M, L	*Gallinula tenebrosa*
Purple Swamphen L	*Porphyrio porphyrio*
Eurasian Coot L	*Fulica atra*

APPENDIX 2

Significances of statistical relationships between waterbirds and wetland variables reported in the text and tables. All relationships were positive except where shown otherwise (–).

Species	r^2	F	df	P
Australian Pelican *Pelecanus conspicillatus*				
Early flood stage				
Wetland area	0.51	11.5	1,9	0.008
Open water	0.45	9.2	1,9	0.014
Late flood stage				
Wetland area	0.31	5.9	1,10	0.036
Open water	0.34	6.7	1,10	0.027
Darter *Anhinga melanogaster*				
Middle flood stage				
Wetland area	0.31	5.8	1,10	0.037
Late flood stage				
Wetland area	0.74	31.9	1,10	0.000
Open water	0.58	16.2	1,10	0.002
Dead gum	0.73	30.7	1,10	0.000
Great Cormorant *Phalacrocorax carbo*				
Early flood stage				
Wetland area	0.49	10.5	1,9	0.010
Late flood stage				
Wetland area	0.73	30.5	1,10	0.000
Open water	0.66	21.9	1,10	0.000
Dead gum	0.72	29.0	1,10	0.000

Appendix 2 — continued.

Species	r^2	F	df	P
Little Black Cormorant *P. sulcirostris*				
Late flood stage				
Wetland area	0.71	28.5	1,10	0.000
Open water	0.47	10.7	1,10	0.008
Dead gum	0.76	34.9	1,10	0.000
Presence of control	0.58	16.2	1,8	0.002
Degree of control	0.61	18.5	1,10	0.002
Prior drying (–)	0.61	13.7	1,7	0.008
Little Pied Cormorant *P. melanoleucos*				
Early flood stage				
Wetland area	0.64	18.9	1,9	0.002
Open water	0.33	5.9	1,9	0.037
Aquatic plants	0.50	10.6	1,9	0.010
Degree of control (–)	0.50	9.1	1,9	0.014
Middle flood stage				
Live gum	0.42	9.1	1,10	0.013
Degree of control (–)	0.34	6.7	1,10	0.027
Late flood stage				
Wetland area	0.53	13.3	1,10	0.005
Dead gum	0.37	7.3	1,10	0.022
Presence of control	0.31	6.0	1,8	0.035
Degree of control	0.32	6.2	1,10	0.032
Pacific Heron *Ardea pacifica*				
Middle flood stage				
Wetland area	0.32	6.2	1,10	0.033
White-faced Heron *A. novaehollandiae*				
Early flood stage				
Wetland area	0.51	11.6	1,9	0.008
Open water	0.41	8.1	1,9	0.019
Aquatic plants	0.45	9.1	1,9	0.015
Presence of control (–)	0.33	5.9	1,7	0.039
Middle flood stage				
Live gum	0.67	23.3	1,10	0.000
Great Egret *Egretta alba*				
Early flood stage				
Wetland area	0.46	9.5	1,9	0.013
Aquatic plants	0.62	17.6	1,9	0.002
Intermediate Egret *E. intermedia*				
Middle flood stage				
Wetland area	0.40	8.4	1,10	0.016
Open water	0.28	5.2	1,10	0.045
Australian White Ibis *Threskiornis molucca*				
Early flood stage				
Aquatic plants	0.53	12.1	1,9	0.007
Prior drying	0.48	7.5	1,6	0.034
Middle flood stage				
Aquatic plants	0.49	11.7	1,10	0.007
Late flood stage				
Aquatic plants	0.30	5.7	1,10	0.038
Straw-necked Ibis *T. spinicollis*				
Early flood stage				
Wetland area	0.38	7.2	1,9	0.025
Live gum	0.38	7.2	1,9	0.025
Yellow-billed Spoonbill *Platalea flavipes*				
Early flood stage				
Wetland area	0.34	6.1	1,9	0.036
Live gum	0.52	11.9	1,9	0.007
Middle flood stage				
Live gum	0.58	16.0	1,10	0.003
Black Swan *Cygnus atratus*				
Middle flood stage				
Aquatic plants	0.40	8.3	1,10	0.016

Species	r^2	F	df	P
Pacific Black Duck *Anas superciliosa*				
Early flood stage				
Wetland area	0.54	12.8	1,9	0.006
Open water	0.32	5.6	1,9	0.042
Aquatic plants	0.39	7.3	1,9	0.024
Presence of control (–)	0.40	7.6	1,7	0.022
Degree of control (–)	0.46	9.6	1,9	0.013
Prior drying	0.47	7.3	1,6	0.036
Late flood stage				
Wetland area	0.46	10.4	1,10	0.009
Live gum	0.27	5.0	1,10	0.050
Dead gum	0.33	6.4	1,10	0.030
Grey Teal *A. gracilis*				
Early flood stage				
Live gum	0.32	5.8	1,9	0.040
Presence of control (–)	0.35	6.5	1,7	0.031
Degree of control (–)	0.57	14.1	1,9	0.005
Middle flood stage				
Aquatic plants	0.30	5.8	1,10	0.037
Presence of control	0.30	5.6	1,10	0.040
Degree of control	0.52	12.7	1,10	0.005
Chestnut Teal *A. castanea*				
Early flood stage				
Aquatic plants	0.39	7.4	1,9	0.024
Degree of control (–)	0.31	5.4	1,9	0.045
Prior drying	0.43	6.3	1,6	0.046
Middle flood stage				
Degree of control (–)	0.36	7.2	1,10	0.023
Australian Wood Duck *Chenonetta jubata*				
Late flood stage				
Live gum	0.29	5.4	1,10	0.042
Prior drying (–)	0.66	16.5	1,7	0.005
All waterbirds				
Early flood stage				
Wetland area	0.46	9.7	1,9	0.013
Open water	0.51	11.4	1,9	0.008
Middle flood stage				
Degree of control (–)	0.39	7.9	1,10	0.018
Late flood stage				
Wetland area	0.42	9.0	1,10	0.013
Open water	0.38	7.6	1,10	0.020
Dead gum	0.35	7.0	1,10	0.025