
Impacts of Livestock Grazing and Tree Clearing on Birds of Woodland and Riparian Habitats

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Abstract: *We investigated the impact of pastoral management on birds in subtropical grassy eucalypt woodland in southeastern Queensland, Australia, where the patterns of land management have made it possible to disentangle the effects of livestock grazing from those of tree clearing. We recorded changes in bird species composition, density, and relative abundance across two woodland habitat types (riparian and nonriparian) and two levels of clearing (wooded and nonwooded) and three levels of livestock grazing (low, moderate, and high) replicated over space (1000 km²) and time (2001–2002). We predicted that species that depend on understory vegetation would be most negatively affected by livestock grazing. A Bayesian generalized linear model showed that the level of grazing had the greatest effect when trees were present. When trees were absent, the impact of grazing was overshadowed by the effects of a lack of trees. Over 65% of species responded to different levels of grazing, and the abundance of 42% of species varied markedly with habitat and grazing. The most common response to grazing was high species relative abundance under low levels of grazing (28% of species), species absence at high levels of grazing (20%), and an increase in abundance with increasing grazing (18%). Despite having similar bird assemblages, the effect of grazing was stronger in riparian habitat than in adjacent woodland habitat. Our results suggest that any level of commercial livestock grazing is detrimental to some woodland birds, particularly the understory-dependant species, as predicted. Nevertheless, provided trees are not cleared, a rich and abundant bird fauna can coexist with moderate levels of grazing. Habitats with high levels of grazing, on the other hand, resulted in a species-poor bird assemblage dominated by birds that are increasing in abundance nationally.*

Keywords: Bayesian GLM, cattle grazing, grassy eucalypt woodland, grazing management, native pasture, Noisy Miner, woodland bird conservation, zero-inflated models

Impactos del Pastoreo de Ganado y la Tala de Árboles sobre Aves de Hábitats Boscosos y Ribereños

Resumen: *Investigamos el impacto de la gestión pastoril sobre aves en un bosque de eucalipto con pasto en el sureste de Queensland, Australia, donde los patrones de gestión de suelos han permitido diferenciar los efectos del pastoreo de los de la tala de árboles. Registramos los cambios en la composición, densidad y abundancia de especies de aves en dos tipos de hábitat (ribereño y no ribereño) y tres niveles de pastoreo de ganado (bajo, moderado y alto) replicados en espacio (1000 km²) y tiempo (2001 y 2002). Pronosticamos que las especies que dependen de la vegetación del sotobosque serían las más afectadas negativamente por el pastoreo de ganado. Un modelo lineal generalizado Bayesiano mostró que el nivel de pastoreo tuvo el mayor efecto cuando había árboles presentes. Cuando no había árboles, el impacto del pastoreo fue eclipsado por los efectos de la falta de árboles. Más de 65% de las especies respondieron a los diferentes niveles de pastoreo, y la abundancia de 42% de las especies varió notablemente con el hábitat y el pastoreo. La respuesta más común al pastoreo fue la abundancia relativa de especies alta cuando los niveles de pastoreo (28% de especies), ausencia de especies en niveles de pastoreo alto (20%) y un aumento en la abundancia con incremento en*

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el pastoreo (18%). No obstante que los ensambles de aves eran similares, el efecto del pastoreo fue mayor en el hábitat ribereño que en el hábitat boscoso adyacente. Tal como se pronosticó, nuestros resultados sugieren que cualquier nivel de pastoreo comercial es perjudicial para algunas aves de bosque, particularmente las especies que dependen del sotobosque. Sin embargo, una fauna de aves rica y abundante puede coexistir con niveles moderados de pastoreo, suponiendo que los árboles no son talados. Por otra parte, los hábitats con altos niveles de pastoreo resultaron con un ensamble de aves pobre en especies, dominado por especies cuya abundancia está incrementando a nivel nacional.

Palabras Clave: bosque de eucalipto con pasto, conservación de aves de bosque, gestión de pastoreo, *Manorina melanocephala*, MLG Bayesianos, modelos sin inflación, pasto nativo, pastoreo de ganado

Introduction

Grazing of domestic livestock is the most extensive use of land globally, both directly through use of pastures and indirectly through production of fodder crops and other feedstuffs (FAO 2002). The removal of woody vegetation is a long-standing practice within the grazing industry (Tepper 1896). Impacts associated with the pastoral industry include alterations in soil health, hydrology, and salinity (e.g., Wood 1924; Williams et al. 1997); changes in vegetation structure and plant species composition and density (e.g., Fensham & Skull 1999; Floyd et al. 2003; McIntyre et al. 2003); and degradation of riparian systems (e.g., Kauffman & Krueger 1984; Schulz & Leininger 1990; Jansen & Robertson 2001a). Early warnings regarding the effects of these factors on bird species (e.g., Barnard 1934; Good & Dambach 1943; Dambach 1944) received little notice. Today scientists continue to document declining faunal communities associated with this pastoral industry (e.g., Bock et al. 1984; Fleischner 1994; Martin et al. 2005a), including declines in birds of woodland, riparian (e.g., Saab et al. 1995; Popotnik & Guiliano 2000; Stanley & Knopf 2002), grassland, and arid (e.g., Baker-Gabb 1998; Gonnet 2001; Pavel 2004) habitats.

Australian landscapes have undergone significant modification for pastoral and agricultural development over the past 200 years, and livestock grazing occurs over 70% of the continent (Freudenberger & Landsberg 2000; NLWA 2002). Grazing effects on bird fauna are complex, and observations are often confounded with other disturbances such as tree clearing (e.g., Abensberg-Traun et al. 1996; Arnold & Weeldenburg 1998; Jansen & Robertson 2001b) or, in arid landscapes, the provision of artificial watering points (James et al. 1999). A further challenge in grazing studies is the difficulty in finding large areas excluded from grazing for long periods (Woinarski & Ash 2002) or significant areas of ungrazed vegetation located on fertile soil (James 2003). Some research results suggest, however, that certain suites of bird species are affected negatively by livestock grazing (Arnold & Weeldenburg 1998; Woinarski & Ash 2002). In particular, species that depend on understory vegetation for foraging and nesting are negatively affected by livestock grazing, whereas species that forage predominantly in the canopy are likely

to be less affected by grazing (Sedgwick & Knopf 1987; Martin & Possingham 2005).

In subtropical eastern Australia commercial grazing occurs in extensively managed grassy eucalypt woodlands, which provided us with an opportunity to quantify independently the role of livestock grazing and tree clearing on the birds of woodland and riparian habitat in a natural landscape experiment. We asked (1) What are the effects of tree clearing on the bird assemblage? (2) What are the effects of grazing on the bird assemblage? and (3) Do birds of different habitats in areas with different levels of tree clearing respond similarly to grazing?

Methods

Study Location

The study region was in the Southeast Queensland Bioregion (Sattler & Williams 1999). The sample area was bounded by 26–28° S and 151–153° E and covered an elevational range of 300–550 m. The climate was subtropical with most rain falling in summer (December to March) and frosts occurring in winter (May to September). Annual rainfall was approximately 640 mm during the study period, below the long-term average of 800 mm (McIvor et al. 2005). Temperature averaged 17–28° C in summer and 5–16° C in winter. The dominant soil types were derived from metamorphic, granite, sandstone, and alluvium landforms.

The vegetation was grassy eucalypt woodland and forest. In many areas the number of trees had been reduced over the last century through ring barking (i.e., removing a ring of bark around the tree stem). More recently, stem-injection of herbicides into trees has become the major management practice to reduce tree density and hence enhance grass production. At the time of our study, over one-third of the study region was wooded and tree regeneration processes were generally active, although there were probably fewer mature trees than prior to European settlement. Overall the landscape state was variegated; that is, native vegetation comprised the majority of the landscape matrix (60–90%, McIntyre & Hobbs 1999). The native vegetation was modified to various

Table 1. Habitat and grazing treatments in an examination of bird species relative abundance in grassy eucalypt woodland.

Habitat	Grazing level	Treatment description
W	1	woodland (wooded nonriparian) intact (exclosures, stock routes): low grazing level; land use indicative of a history of no, little, or infrequent domestic livestock grazing or cessation of grazing for over 10 years; grass swards intact; native trees, shrubs present; background marsupial grazing present
W	2	woodland modified (in paddock): moderately grazed; large native tussock grass structure and short grazed patches, indicating selective grazing; majority of shrub layer absent
W	3	woodland modified (in paddock): highly grazed, closely cropped, lawn-like understory dominated by stoloniferous/rhizomatous grasses, indicating prolonged nonselective grazing; shrub layer absent
R	1	riparian (wooded nonriparian) vegetation intact (exclosures): low levels of grazing (as for W1); tree, shrub, and herbaceous layer present, surrounded by vegetation consistent with W1
R	2	riparian vegetation modified (in paddock): moderately grazed (as for W2) surrounded by vegetation consistent with W2
R	3	riparian vegetation modified (in paddock): highly grazed (as for W3) surrounded by vegetation consistent with W3
O	2	cleared riparian (in paddock): all trees removed, native pasture ground layer; moderately grazed, large native tussock grass structure and short grazed patches, indicating selective grazing
O	3	cleared riparian (in paddock): as above, heavily grazed, closely cropped, lawn-like understory structure
N	1	native pasture (cleared nonriparian) (exclosures): cleared woodland, tree and shrub layer removed; low grazing; land use indicative of a history of no, little, or infrequent grazing, grass swards intact
N	2	native pasture (in paddock): cleared woodland, tree and shrub layer removed; moderately grazed (as for O2)
N	3	native pasture (in paddock): cleared woodland, tree and shrub layer removed; heavily grazed (as for O3)

degrees by grazing and other disturbances, but overall intensive land uses such as cropping and sown pasture were limited. The most abundant eucalypts were *Eucalyptus crebra* F. Meull., *E. melanophloia* F. Muell., and on bottomland, *E. tereticornis* Smith (Martin et al. 2000). Shrub densities were low overall but highest on upland metamorphic and sandstone landforms. The most abundant shrub within this landscape was the exotic shrub, *Lantana camara* L.

Site Selection

Our primary objective was to observe how grazing of the understory vegetation influences bird species abundance, density, and composition when controlling for tree density. We ascertained the grazing history of a site through discussions with landholders and cross-checked our assessment against the present structural condition and composition of the grass sward. Sward structure and composition is an indicator of grazing history in this ecosystem (McIntyre et al. 2003; McIvor et al. 2005). Based on our assessment results, we categorized sites into one of the three levels of grazing: low (history of no to low-level grazing, grass swards intact); moderate (selective grazing); and high (nonselective grazing) (levels further defined in Table 1 and shown in Fig. 1). Background native marsupial grazing was present across all grazing levels. Further information on the clearing history, landscape context, vegetation composition, and structure of the study sites can be found in McIntyre et al. (2003), McIntyre and Martin (2001), and Martin et al. (2006).

Two tree densities (wooded and cleared) and two woodland habitats (riparian and nonriparian) were sam-

pled. Together with grazing, these treatments resulted in 12 ($2 \times 2 \times 3$) factorial combinations. With the exception of one grazing and habitat combination, low levels of grazing in cleared riparian habitat, all other combinations were available for examination. We used stratified random sampling to select 8 replicates of each of the 11 treatments, for a total of 88 sites. Sites were located across an area of 1000 km². Distance between sites was a minimum of 1 km. All sites contained a native understory and had a history of no fertilization.

In cleared sites all trees and shrubs had been removed. Uncleared sites had a woodland structure, with a relatively uniform density of trees, although woodland sites with low-level grazing had a higher tree basal area than highly grazed riparian sites (Fig. 2). The exotic shrub *Lantana camara* was present in all wooded sites and the proportion of a site covered by shrubs was highly correlated with the proportion of a site covered by *Lantana* (Pearson's correlation coefficient = 0.82, $p < 0.001$). For a site to be considered for sampling the appropriate combination of grazing level and clearing level had to overlap over a minimum of 20 ha.

Riparian habitats were situated alongside third- and fourth-order watercourses as determined from the Australian Surveying and Land Information Group 1:250 000 maps. Half the sites contained permanent water and half were ephemeral (these were split evenly between cleared, wooded, and grazing treatments). Wooded riparian sites were situated within woodlands with a grazing level that corresponded to the sampled riparian site.

Terms used to describe the clearing and habitat variables for sites are as follows: *native pasture* (cleared nonriparian); *woodland* (wooded nonriparian), *riparian*

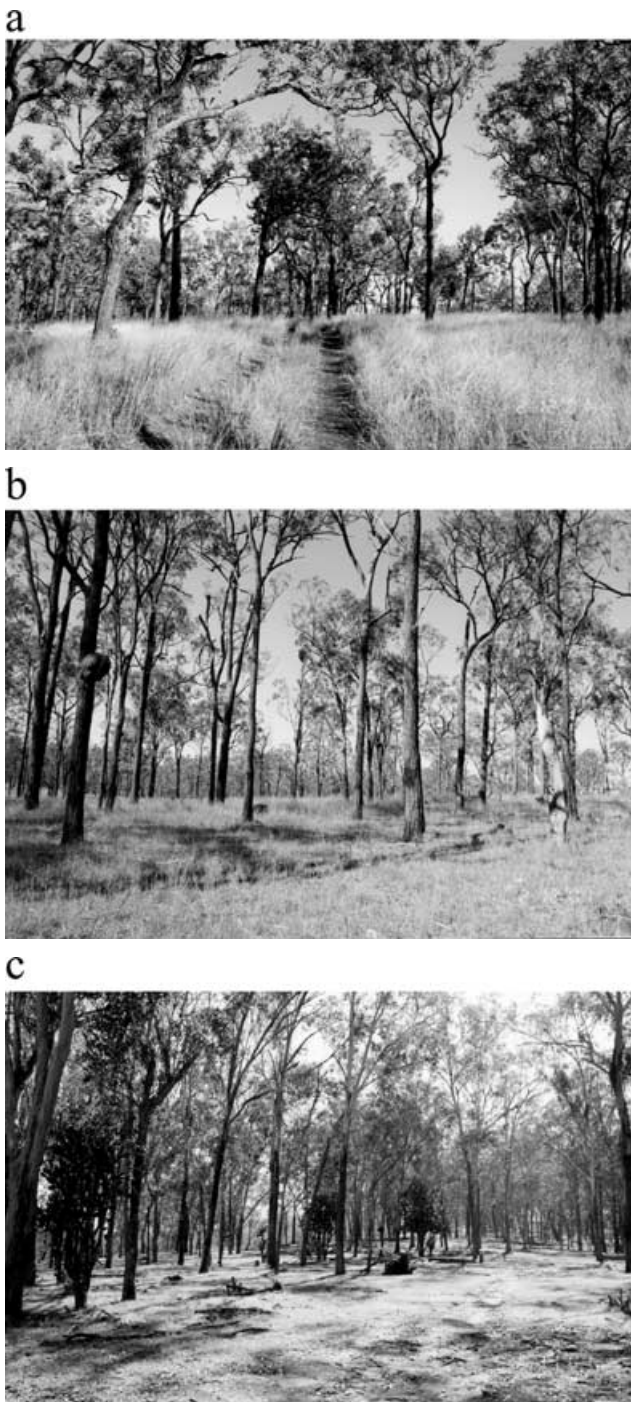


Figure 1. Study area in subtropical grassy eucalypt woodland in southeastern Queensland, Australia: (a) woodland with low-level grazing, (b) moderately grazed woodland, and (c) highly grazed woodland.

(wooded riparian), and *cleared riparian*. Native pasture although composed of native grassland species was not strictly a native grassland; rather, it was the grassy understorey of woodland that was cleared to facilitate grazing. All sites are described individually in Table 1.

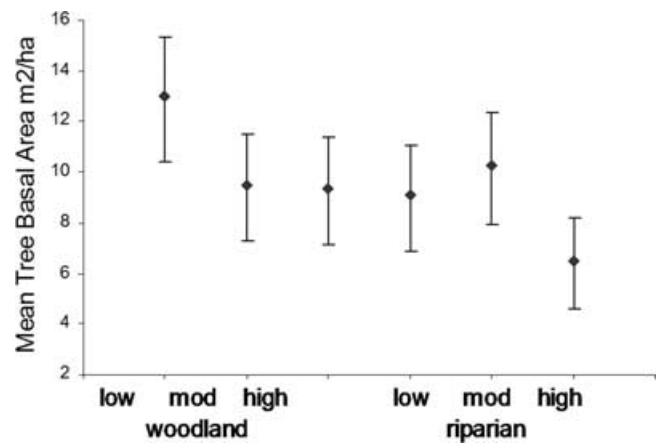


Figure 2. Mean estimate of tree basal area for wooded study sites at three grazing levels (low, moderate, high). Bars represent 95% credible intervals.

Bird Sampling

We adapted the standard 2-ha-area search technique (Barrett et al. 2003) for this study. Within each of the 88 sites a 2-ha search area was located near the center of the 20-ha area consisting of the same treatment and was traversed by a single observer (T.M.). The abundance of all bird species seen or heard within this area was recorded during a 20-minute period. Surveys were repeated on two different days, at a minimum of 4 weeks apart, in each season (summer and winter), for a total of 352 site visits. Thus we had 1 year of observations for each season evaluated. With the exception of aerial feeders (swifts, swallows, and raptors), all birds flying at 20 m or above were excluded. We summed bird records across the two visits to provide an index of the intensity of use of each site by each bird species in each season, yielding a measure of relative abundance.

Bird counts were made on fine mornings in summer (November–January 2001–2002) between 0445 and 0945 hours and in winter (June–July 2002) between 0645 and 1145 hours. Surveys were not conducted when the temperature rose above 35°C or went below –2°C. To avoid possible sampling biases, we used a restricted random visitation method (Mac Nally & Horrocks 2002). This involved partitioning the entire survey region into six geographical groups and visiting each region and subsequent sites within each region randomly. Bird nomenclature follows Christidis and Boles (1994).

Species detectability is an important and often overlooked issue (Rosenstock et al. 2002; Tyre et al. 2003); the implications of imperfect detection on model parameters and ecological inference are reviewed in Martin et al. (2005b). Rosenstock et al. (2002) outline three factors that may result in an index of counts with no consistent positive correlation with actual bird density: (1) differences in observer performance, (2) environmental

variables that affect bird behavior and observer efficiency given these variables, and (3) behavioral attributes of the birds themselves.

We satisfied all three of these factors and hence did not correct for detectability. A single observer with over 10 years experience observing birds within the study region undertook all records, avoiding the possibility of biases due to observer performance. The probability of detecting a bird could vary with grazing level; however, the open structure of grassy eucalypt woodlands, sparse shrub layer (McIntyre et al. 2003), standardizing of tree density, and the high number of records based on calls rather than sightings minimized the chance of this affecting our data. In addition, we compared the same vegetation type (grassy eucalypt woodland) in three different grazing treatments, not in different vegetation types (e.g., rainforest vs. woodland) (Fig. 1). It is also possible that different birds had different detection rates due to their behavior. Even if this bias were present, we contend it would be equal across grazing treatments and therefore would not affect our conclusions. Finally, the randomization of sampling blocks over time and space helped minimize potential biases associated with treatment, time of day, or date.

Data Analysis

INDIVIDUAL SPECIES, SPECIES DENSITY, AND RELATIVE ABUNDANCE RESPONSES

We analyzed individual species, species density, and relative abundance responses with a Bayesian generalized-linear fixed-effects factorial model. Two levels of grazing (moderate and high) were investigated across all four habitats, and all three levels of grazing (low, moderate, and high) were investigated across three habitats (woodland, riparian, and native pasture). We used freeware software WinBUGs (Spiegelhalter et al. 2003) to fit the models.

Count data are most commonly modeled using a Poisson distribution, but some of the counts for species in our data set exhibited more zeros than a Poisson or negative binomial distribution could accommodate (Welsh et al. 1996; Cameron & Trivedi 1998; Martin et al. 2005b). In these cases we modeled the species as a mixture of two distributions, capturing two underlying processes: a process leading to excess zeros, modeled as a point mass at zero, and a process leading to counts of species, modeled as a Poisson distribution. This is referred to as a zero-inflated Poisson (ZIP) mixture model (Lambert 1992).

With the ZIP-mixture modeling approach, the probability (P) that a zero is generated through the Poisson distribution is represented by the mixture probability $p(x)$, where the mean abundance of a species at a site for the Poisson component is represented by $\lambda(z)$ (x and z represent covariate matrices).

$$P(y = 0|x, z) = 1 - p(x) + p(x) \exp(-\lambda(z)),$$

$$P(y = r|x, z) = p(x) \exp(-\lambda(z)) \lambda(z)^r / r!, \quad (1)$$

$$\text{and } r = 1, 2, \dots,$$

where $p(x)$ is the probability that the number of birds at a site is generated through a Poisson distribution and given that the counts are generated through a Poisson distribution, $\lambda(z)$ is the mean number of birds at a site. A logit and log-linear link are used to model $p(x)$ and $\lambda(z)$, respectively, with covariates x and z potentially differing (Lambert 1992; Dalrymple et al. 2003). By multiplying the mixing probability $p(x)$ by $\lambda(z)$, a relative abundance estimate is generated.

We analyzed summer and winter migrant species in the season in which they occurred (88 sites). Only species with a frequency >6% were included in the analysis of the generalized linear model (GLM).

BIRD-SPECIES ASSEMBLAGE RESPONSE

We used multivariate ordination analyses to compare bird species assemblages between the habitat and grazing treatments. Only species that occurred at a minimum of four sites (3%) in either season were included in these analyses to reduce the level of noise. Nonmetric multidimensional scaling (MDS) ordinations were performed using the PRIMER package (Clarke & Gorley 2001) with the Bray-Curtis similarity measure (Clarke 1993). We tested whether the variation in bird species composition between treatments was greater than the variation within treatments (Carr 1996) with analysis of similarities (ANOSIM).

Results

Species Abundance and Density

Across all habitats, grazing levels, and seasons, 138 species and 8418 individuals were recorded. More species were recorded in summer (126 species, 4010 individuals) than in winter (92 species, 4408 individuals; Fig. 3a), although in winter more individuals were recorded. The number of species detected varied substantially between all four habitats, with the greatest number of species in riparian habitats followed by woodland and cleared riparian. The lowest species density was in native pasture. Seasonal variation in the number of species detected and relative abundance were most pronounced in woodland and riparian sites due to large turnovers in summer and winter migrant species. There was an interaction between habitat and grazing, with density generally declining with increasing grazing intensity in woodland, riparian, and cleared riparian sites, whereas density increased slightly with grazing in native pasture habitat.

Irrespective of grazing level, species relative abundance declined from riparian to woodland to cleared riparian and native pasture, with the two latter habitats sharing similar estimates of relative abundance. Patterns of species relative abundance for cleared riparian and native pasture sites mirrored that of species density (Fig. 3b). Nevertheless, within low and moderate grazing in woodland and riparian sites, substantially more individuals were recorded in winter despite fewer species being recorded. This change can be largely attributed to many species occurring at low frequencies (<6%) in summer but not in winter (e.g., Banded Lapwing [*Vanellus tricolor*], Spotted Quail Thrush [*Cinlosoma punctatum*], Azure Kingfisher [*Alcedo azurea*], Grey-crowned Babbler [*Pomatostomus temporalis*], White-winged Chough [*Corcorax melanorhambhos*]). Estimates of relative abundance in winter were augmented by large numbers of individuals of several migrant species (e.g., Golden Whistler [*Pachycephala pectoralis*], Grey Fantail [*Rhipidura fuliginosa*], Rose Robin [*Petroica rosea*]).

Birds in wooded riparian sites showed the most dramatic decline in relative abundance with increasing grazing pressure; sites with low-level grazing contained twice as many individuals as highly grazed sites. Similar to

species density, there was an interaction between grazing and habitat, with relative abundance increasing in native pasture sites with increasing grazing pressure, which was contrary to the pattern of decline in relative abundance in the other three habitats.

Species-Specific Responses

Sixty species were analyzed individually with a Bayesian GLM with grazing, habitat, season, and interaction terms. From the GLM results we identified several types of species responses to grazing, ranging from a substantial decline in relative abundance with increasing grazing pressure to an increase in relative abundance with increasing grazing pressure. Estimates of relative abundance of 47 species across the four habitat types revealed clear species preferences for either wooded or cleared habitat. Relative abundance estimates of 39 species varied with grazing level, and estimates of 25 species varied with grazing and habitat type; hence, species responses to grazing were often habitat dependant. A full list of bird species, their frequencies of occurrence, estimates of relative abundance, and responses to grazing, habitat, and season are available from T.M.

RESPONSES TO GRAZING

Eleven species showed a substantial decrease in relative abundance with increasing grazing pressure (e.g., low to high grazing) in at least one habitat type and included understory-foraging species (Brown Thornbill [*Acanthiza pusilla*], Variegated Fairy-Wren [*Malurus lamberti*], White-browed [Scrubwren *Sericornis frontalis*]) and midcanopy and canopy foragers (Buff-rumped [Thornbill *Acanthiza reguloides*], Yellow-faced Honeyeater [*Lichenostomus chrysops*], Lewin's Honeyeater [*Meliphaga lewinii*], White-throated Honeyeater [*Melithreptus albogularis*], Grey Fantail [*Rhipidura fuliginosa*], Silveryeye [*Zosterops lateralis*], Spotted Pardalote [*Pardalotus punctatus*]). The Red-backed Fairy-Wren [*Malurus melancephalus*], an understory specialist, exhibited this response in native pasture only.

Another 15 species were intolerant of high levels of grazing in at least one habitat (not recorded at highly grazed sites) and had either similar estimates of abundance under low and moderate levels of grazing (e.g., Eastern Whipbird [*Psophodes olivaceus*], White-throated Treecreeper [*Cormobates affinis*], Leaden Flycatcher [*Myiagra rubecula*]), or substantially higher abundance estimates under low as opposed to moderate levels of grazing (e.g., Brown Gerygone [*Gerygone mouki*], Scarlet Honeyeater [*Myzomela sanguinolenta*]). Four species had similar relative abundance under low and moderate grazing but substantially lower relative abundance under high grazing (e.g., Noisy Friarbird [*Ptilinopus corniculatus*], Red-browed Finch [*Neochmia temporalis*]).

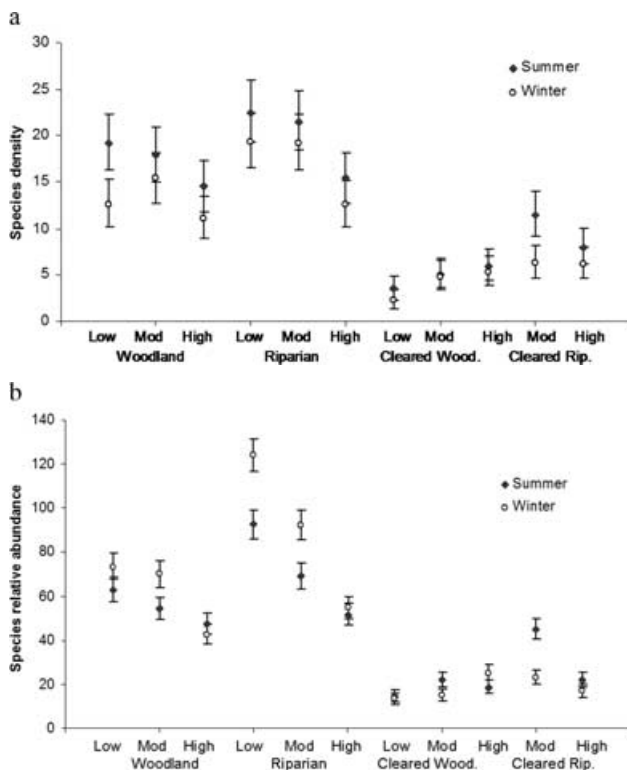


Figure 3. Mean estimates of (a) total number of bird species (density) and (b) total number of relative bird abundance across the grazing treatments (low, moderate, high) in 11 habitats with 95% credible intervals.

Eight species increased in density under moderate levels of grazing compared with low or high grazing levels in at least one habitat (e.g., Sacred Kingfisher [*Todiramphus sanctus*], Jacky Winter [*Microeca fascians*], Fuscous Honeyeater [*Lichenostomus fuscus*]).

Estimates of abundance for 13 species increased markedly with increasing grazing pressure under at least one habitat and with the exception of the Noisy Miner (*Manorina melanocephala*) were dominated by ground-foraging species (e.g., Australian Wood Duck [*Chenonetta jubata*], Galah [*Cacatua roseicapilla*]). Several of these species occurred only in moderate and highly grazed habitats (e.g., Masked Lapwing [*Vanellus miles*], Crested Pigeon [*Ocyphaps lophotes*]).

HABITAT AND GRAZING INTERACTION

Some species' responses to grazing varied substantially with habitat type (e.g., Golden Whistler [*Pachycephala pectoralis*]). These species had similar densities across all three grazing treatments in woodland but a marked decline in abundance with increasing grazing pressure in riparian habitats. Several understory and canopy specialists were intolerant of high levels of grazing in woodland but occurred in highly grazed sites in riparian habitat, though at reduced densities.

LOW-DENSITY SPECIES

The densities of 78 bird species were too low to analyze statistically. Most occurred only at low and/or moderate levels of grazing in woodland or riparian sites (e.g., Grey-crowned Babbler [*Pomatostomus temporalis*], Dusky Woodswallow [*Artamus cynopterus*], Black-chinned Honeyeater [*Melithreptus gularis*]) or in native pasture sites (e.g., Banded Lapwing [*Vanellus*

tricolor], Singing Bushlark [*Mirafra javanica*]). Low-density species recorded in highly grazed habitats included the White-winged Chough (*Corcorax melanorhambos*) and Apostlebird (*Struthidea cinerea*).

Species Assemblage Response

The ordination (Fig. 4) clearly separated wooded sites (woodland and riparian) from nonwooded sites (cleared riparian and native pasture). The second split, although less pronounced, was between the grazing levels, with sites with low-level grazing tending to fall out toward the top of the ordination and highly grazed sites falling out near the bottom. Between the wooded and nonwooded sites were a few highly grazed woodland (W3) and riparian (R3) sites, suggesting that these sites tended to share similarities to cleared riparian and native pasture sites in terms of their species composition. Overlaying the density of the Noisy Miner (*Manorina melanocephala*) (shaded circles on the ordination), a native honeyeater known for its competitive exclusion of other bird species (Grey et al. 1997; Piper & Catterall 2003), showed that its highest densities were at these highly grazed woodland and riparian sites. Separate ordinations for summer and winter showed a similar pattern.

Pairwise ANOSIM results confirmed that the bird assemblages of the 11 habitat and grazing treatments were significantly different from one another with three exceptions (Table 2). Moderately grazed cleared riparian (O2) and highly grazed cleared riparian (O3) sites, moderately grazed riparian (R2) and moderately grazed woodland (W2) sites, and highly grazed native pasture (N3) sites and highly grazed cleared riparian (O3) sites were most similar to one another in terms of their bird species assemblages.

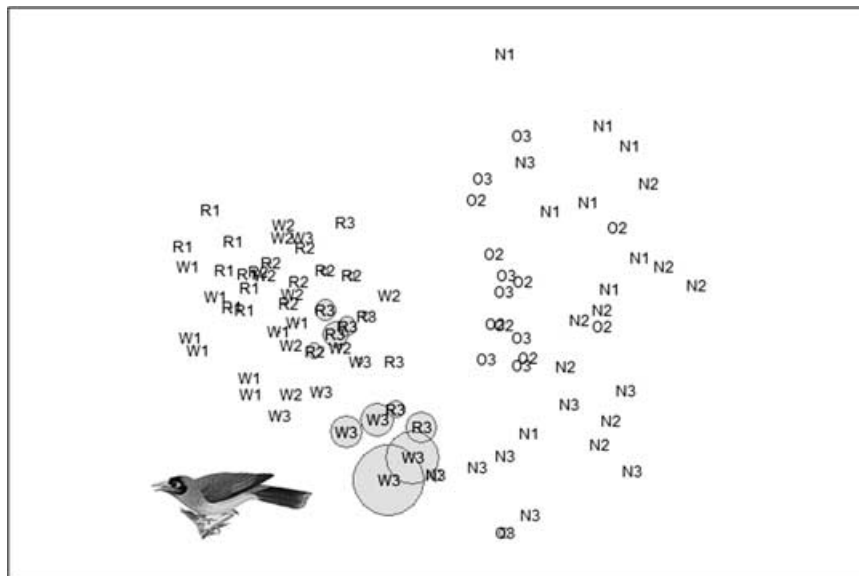


Figure 4. Multidimensional scaling (MDS) ordination of bird species composition (presence/absence) for summer and winter combined. Species composition was similar among habitat and grazing treatments based on Bray Curtis dissimilarity measure (two-dimensional stress = 0.18, three-dimensional = 0.13), where W, woodland; R, riparian; N, nonwooded riparian; O, native pasture, and grazing is defined as 1, low; 2, moderate; 3, high). Shaded circles represent the density of Noisy Miner (pictured on ordination) at a given treatment, with increasing density depicted by increasing bubble size.

Table 2. Results of one-way analysis of similarities (ANOSIM, global $R = 0.655$, $p = 0.01$) pairwise tests between the habitat and grazing treatments.

Habitat and grazing level ^a	Native pasture (N)			Cleared riparian (O)		Riparian (R)			Woodland (W)		
	N1	N2	N3	O2	O3	R1	R2	R3	W1	W2	W3
N1	—	0.001	0.002	0.001	0.001	0.001	0.002	0.001	0.001	0.001	0.001
N2		—	0.002	0.007	0.01	0.001	0.001	0.002	0.002	0.001	0.001
N3			—	0.001	0.072 ^b	0.002	0.001	0.002	0.001	0.001	0.001
O2				—	0.382 ^b	0.001	0.001	0.001	0.001	0.001	0.001
O3					—	0.001	0.001	0.002	0.001	0.001	0.001
R1						—	0.001	0.001	0.026	0.002	0.001
R2							—	0.001	0.002	0.123 ^b	0.002
R3								—	0.001	0.001	0.046
W1									—	0.006	0.006
W2										—	0.001
W3											—

^aGrazing level is 1, low; 2, moderate; 3, high. Letters are habitat types as described in Table 1.

^bHabitat and grazing treatments not significantly different from one another.

Discussion

Effects of Tree Clearing

Clearing of native vegetation has a dramatic influence on bird assemblages, with cleared habitats containing distinctly different and species-poor bird assemblages, a finding demonstrated in many other studies (e.g., Saunders 1989; Wilcove & Robinson 1990; Villard 1999). Our results also support this finding: the greatest difference in the bird assemblage was associated with the removal of woody vegetation (Fig. 4).

Effects of Grazing on Birds Independent of Tree Clearing

The influence of livestock grazing on the bird assemblages of all habitats we examined was also strong; the most striking difference was between sites that had low levels of grazing and those with high levels. Highly grazed woodland and riparian, and to a lesser extent native pasture habitats, contained a distinct bird assemblage from that of habitats that had low or moderate levels of grazing (Fig. 4; Table 2). Although there was greater overlap in the species composition of sites with low and moderate levels of grazing across habitats, substantial differences in the species composition and relative abundance estimates among these grazing regimes in each habitat were recorded, suggesting that any level of commercial grazing will negatively affect some bird species.

Low levels of grazing supported substantially higher densities of several species that have been characterized by Catterall et al. (1998), in a study in the same bioregion, as dependent on bushland due to their increased probability of occurrence in forest or woodland with an understory of shrubs or grasses. The increased structural complexity (saplings, shrubs, large tussock grasses) as a

result of exclusion of commercial levels of grazing in sites with low-level grazing appears to benefit these species.

Several birds declining elsewhere in Australia (Reid 1999; Garnett & Crowley 2000; Barrett et al. 2003) as a result of habitat loss and modification were found in highest densities in moderately grazed habitat. In the absence of changes in tree cover, these bird species responded positively to moderate levels of grazing. Livestock grazing may be replacing the natural disturbances caused by fire and macropod grazing in which these species specialized. This is an important finding because their decline has tended to be attributed to any level of livestock grazing (Garnett & Crowley 2000). Other grassy woodland birds that are declining nationally were recorded at low densities at sites with low and moderate levels of grazing, suggesting that grazing may be only one of many factors responsible for their decline.

The distinct suite of birds recorded in highly grazed sites are among a group of ground-foraging species (Martin & Possingham 2005) increasing nationally (Blakers et al. 1984; Barrett et al. 2003) and associated with highly modified landscapes. Nevertheless, the differences in bird assemblages of highly grazed woodlands and to a lesser extent highly grazed riparian zones cannot necessarily be attributed to grazing alone. The abundance of hyper-aggressive Noisy Miners was greatest in highly grazed woodland and riparian sites (Fig. 3). Therefore the overall bird assemblage of these woodlands and riparian habitats is probably the result of both direct changes to habitat by grazing and the effect of increased numbers of Noisy Miners. In southern Australia densities of Noisy Miners are positively correlated with grazing intensity (Loyn 1987). In contrast on the southwestern and northwestern edges of the Noisy Miner's range densities of this species are highest in ungrazed habitat. Jansen and Robertson (2001b) found lower densities of Noisy Miners with heavy grazing; however, their most heavily grazed

sites also contained few trees. In northern Australia the Noisy Miner is more abundant in ungrazed areas with the congeneric Yellow-throated Miner (*Manorina flavigula*) dominating grazed sites (Woinarski & Ash 2002).

Below-average rainfall for several years proceeding and including the study period resulted in poor growing conditions for grasses in particular (McIvor et al. 2005) and may have contributed to more pronounced effects of grazing. During times of drought ungrazed habitats provide critical refuge for wildlife (Recher & Lim 1990).

Interactions between Habitat and Grazing

In native pastures bird species density and relative abundance were lowest in low-grazed habitats. In our study area there were no areas of natural grassland; instead, there was grassy woodland cleared of its trees, referred to as native pasture. Therefore, there is no native bird assemblage in the region that specialized in native grassland. The few species that have benefited from tree removal at sites with low-level grazing are grassy woodland species (e.g., Singing Bushlark). The lawn-like structure of highly grazed native pasture is an appealing foraging habitat for several species found throughout developed areas of Australia, including the Crested Pigeon, Masked Lapwing, Torresian Crow (*Corvus orru*), and Australian Magpie (*Gymnorhina tibicen*). Woinarski and Ash (2002) also found higher densities of these species in grazed habitat.

The degree of decline in estimates of species density and relative abundance with increasing grazing pressure were considerably steeper in riparian habitat compared with woodland. Nevertheless, excluding birds that forage predominantly in or around water, the composition of the assemblages was very similar. This suggests that the effect of grazing is greater in riparian areas than in woodland (Fig. 4a & 4b). The vegetation of sites with low levels of grazing is generally more structurally diverse than intact woodland habitats. The reduction in structural complexity caused by grazing is therefore more pronounced in riparian habitats. In our study moderate and high levels of grazing tended to make riparian habitats more like woodland habitats in both vegetation structure and bird-fauna assemblage (Table 2). Riparian areas represent <3% of the regional landscape, yet cattle spend a disproportionately large amount of time foraging, drinking, and resting in these habitats. The deleterious effects of cattle on wetlands, riparian habitats, and waterways and their associated flora and fauna have been well documented (e.g., Knopf et al. 1988; Dobkin et al. 1998; Krueper et al. 2003).

Mechanisms Underlying Bird Response to Grazing

Altered foraging and nesting opportunities as a result of changes in the vegetation structure and composition caused by grazing have been hypothesized as key mechanisms underlying bird response to livestock grazing. In

a related study in the same study region, bird species preferring foraging height was a significant predictor of that species' susceptibility to livestock grazing (Martin & Possingham 2005). Species that foraged predominantly within the understory vegetation, the strata most affected by grazing, declined in relative abundance with increasing levels of livestock grazing, whereas those species that foraged primarily on the ground tended to increase.

Nesting behavior including preferred nest height is also likely to contribute to species susceptibility to grazing, although perhaps less so than foraging behavior because nesting only occurs for a limited portion of the year, whereas birds require forage daily. Nevertheless, the relative importance of nesting behavior and other variables in explaining the response of bird species to livestock grazing have yet to be tested.

Historical and Delayed Impacts of Grazing

Although tree basal area was similar across all habitats, current tree size and density within woodlands were likely different before commercial grazing began some 200 years ago. Even our low-level grazing sites have had some level of domestic grazing and tree removal over a long period of time. The removal of hollow-bearing trees for timber, altered fire regimes, and grazing of domestic livestock are likely to have long-term effects on tree health and demography regardless of physical tree clearing or thinning (Bezkorowajnyj et al. 1993). It is difficult to know how close present avifauna resembles early pastoral times (Barnard 1925; Barnard 1934; Woinarski & Catterall 2004). Species most sensitive to livestock grazing, loss of large trees, clearing of fertile lands, and broad-scale clearing elsewhere in Australia are likely to have already been lost from these landscapes (e.g., Paradise Parrot [*Psephotus pulcherrimus*], Crested Bellbird [*Oreoica gutturalis*]). For other species there may be a long time lag between livestock grazing, tree clearing, and local bird extinction (Brooks et al. 1999).

Future Threats

Two additional processes threaten to intensify the use of grazed landscapes and in turn negatively affect Australian woodland bird fauna. Rising global demand for livestock products is increasing the pressure for extensive grazing operations to become more intensive (Krebs et al. 1999; FAO 2002). This could result in further vegetation clearing, replacement of native pastures with sown pastures, broad-scale use of fertilizers and irrigation, and greater demand to graze properties at high levels. A second threat, peri-urban encroachment is consuming both agricultural and grazing land close to major urban centers (Greene & Stager 2001). This has the potential to intensify the use of these areas and forces agriculture and grazing into less-fertile landscapes that currently act as critical refuge for woodland birds.

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