

Predicting the impact of livestock grazing on birds using foraging height data

TARA G. MARTIN*†‡ and HUGH P. POSSINGHAM*

*The Ecology Centre, School of Life Sciences, University of Queensland, St Lucia, Brisbane, Queensland 4072, Australia; and †CSIRO Sustainable Ecosystems, QBP, 306 Carmody Rd, St Lucia, Queensland 4067, Australia

Summary

1. Habitat structure is a major determinant of bird species diversity. One process by which habitat structure is altered is livestock grazing, the most extensive land use across most continents. While the impacts of grazing on vegetation have received much attention, the effects on avifauna are less well known.

2. Predictions of the impact of grazing on Australian woodland and riparian bird assemblages were formulated. We used available information on the vegetation strata utilized by each species for foraging and the strata most affected by grazing.

3. We compared predictions based on foraging height preferences with differences in bird density in grassy eucalypt woodland and riparian habitats subject to three levels of grazing. We found that foraging height preference was a good predictor of species' susceptibility to grazing. Birds exhibited both monotonic and non-monotonic responses to grazing, with the majority of bird species declining with increasing grazing pressure.

4. *Synthesis and applications.* Existing information on foraging behaviour can be used to make predictions of the impact of any threat on birds where that threat alters habitat structure. While the approach is simple, it is a point of departure for more complex predictive models, and avoids the circularity of *post hoc* interpretation of impact data. This approach can be used to guide management decisions where landscapes are in a state of transition and species conservation is a priority.

Key-words: bird conservation, foraging behaviour, habitat structure, pastoral management, predictive model

Journal of Applied Ecology (2005) **42**, 400–408
doi: 10.1111/j.1365-2664.2005.01012.x

Introduction

For decades ecologists have collected data on where and how birds forage. These data have typically been used to understand patterns in community structure (Hartley 1953; MacArthur 1958; Recher *et al.* 1985; Ford, Noske & Bridges 1986) and interspecific competition (Cody 1974). We have used bird foraging height data in a novel way to predict the impact of habitat alteration.

Grazing by livestock is one process that alters habitat structure. Pioneering work by Dambach & Good (1940), Good & Dambach (1943) and Dambach (1944) demonstrated the deleterious impacts of livestock grazing on understorey vegetation and subsequent breeding

bird populations in the woodlands of Ohio, USA. Despite this early work and the extensive nature of livestock grazing globally, the degree to which changes in vegetation composition and structure caused by livestock grazing influence native faunal assemblages remains largely unknown. Current research on impacts of grazing on woodland and riparian bird fauna uses a classical null hypothesis testing approach, assuming there is no impact, and attempts to reject that hypothesis (Knopf, Sedwick & Cannon 1988; Popotnik & Guiliano 2000; Soderstrom, Part & Linnarsson 2001; Stanley & Knopf 2002; Woinarski & Ash 2002; James 2003; Krueper, Bart & Rich 2003). None of these studies explicitly tests mechanisms underlying bird susceptibility to grazing but rather make *post hoc* inferences regarding possible causes. Other studies predict a priori bird species likely to be most affected by grazing (Sedgwick & Knopf 1987) or changes in forest structure (Haila, Järvinen & Väisänen 1980) but do not test the

‡Correspondence: Tara Martin, CSIRO Sustainable Ecosystems, Queensland Bioscience Precinct, 306 Carmody Road, St Lucia, Queensland 4067, Australia (e-mail Tara.Martin@csiro.au).

underlying reasons that led to the prediction in the first place. Understanding the effects of grazing on Australian woodland and riparian birds has also been hindered by the confounding effect of grazing intensity with changes in tree density, as these are often linked (Abensberg-Traun *et al.* 1996; Arnold & Weeldenburg 1998; Ludwig *et al.* 2000; Jansen & Robertson 2001; Woinarski & Catterall 2004). Nonetheless, grazing has been implicated in the decline of woodland and riparian birds (Dambach 1944; Jansen, Little & Crowe 1999; Recher 1999; Garnett & Crowley 2000; Popotnik & Guiliano 2000; Traill & Duncan 2000) and recent studies lend support to this hypothesis (Martin *et al.* 2005; Woinarski & Ash 2002). However, the mechanisms underlying these declines remain to be tested. Using foraging data we explored one of the mechanisms underlying bird susceptibility to grazing.

Bird species richness has long been linked to habitat characteristics, in particular structural complexity (MacArthur & MacArthur 1961; MacArthur 1964; Cody 1968; Recher 1969; Willson 1974). Generally, habitats with a complex architecture support more species than habitats with a simple architecture because they provide more resources and/or opportunities for microhabitat segregation (Bell, McCoy & Mushinsky 1991; MacArthur, Recher & Cody 1966; Vickery *et al.* 2001). Thus more species may co-occur per unit area, leading to a positive correlation between biological diversity and structural diversity (MacNally *et al.* 2001). A variety of elements contribute to habitat structure (Rice, Anderson & Ohmart 1984; Bell, McCoy & Mushinsky 1991), including vertical and horizontal zonation and patchiness of the vegetation (Willson 1974), floristic elements (Woinarski, Tidemann & Kerin 1988), structural elements of vegetation, such as the distribution and size of trees (MacNally 1990), and provision of resources. Ground cover and litter are also key components of structural diversity (Recher 1991; Abensberg-Traun & Smith 1993; Martin & Green 2002).

Grazing of woodland and riparian habitats alters the vertical and horizontal structure and composition of vegetation through a combination of trampling, grazing, changes in nutrient fluxes and loss or altered recruitment (reviewed by Fensham & Skull 1999; Kauffman & Krueger 1984; McIntyre, Heard & Martin 2002, 2003). Generally, shrubs are removed, establishment of tree seedlings is inhibited, saplings are trampled and browsed, and the grass layer is grazed in a heterogeneous manner or, when grazing pressure is heavy, the grass sward becomes homogeneous (McIntyre, Heard

& Martin 2003). Hence we predicted that species that preferentially forage in the understorey habitat are more likely to be adversely affected by grazing than species using the canopy or foraging on the ground.

Using this simple assumption, we built an impact-of-grazing model whereby foraging height preferences are used to predict the effect of livestock grazing by relating the height at which a bird predominantly forages with its susceptibility to grazing. These predictions were made before any field data were collected. The model was tested with field data collected from landscapes with similar canopy cover, hence the differential response is interpreted as a consequence of changes in the understorey caused by livestock grazing. This approach allowed us to test whether the foraging behaviour of a bird species is a good predictor of its vulnerability to grazing. We tested this model on field data collected from two types of habitat impacted by grazing: riparian vegetation and adjacent grassy eucalypt woodland.

The model

The changes in vegetation structure and composition brought about by livestock grazing are likely to impact bird foraging differentially in certain strata. We obtained published information on foraging time–budget data for Australian birds in woodlands similar to those in our study area (see the Appendix). Using these data we estimated the proportion of time different bird species spent foraging in various vegetation strata. The specification of foraging height categories was based on the literature and our observations of grazing impacts on different vegetation elements (Table 1). Where data from woodlands in eastern Australia were not available, data from structurally similar woodlands in other regions were used (Recher & Davis 1998; Tibbetts & Pruett-Jones 1999).

MODEL ASSUMPTIONS

In developing the impact-of-grazing model we made the following assumptions based on empirical grazing studies (McIntyre, Heard & Martin 2003; McIvor *et al.* 2005) and personal observations. (i) Grazing reduces the grass/tussock layer and shrub/sapling layer (i.e. understorey). (ii) Grazing increases the amount of bare ground and short grass. (iii) Grazing has a negligible effect on the canopy layer (although in the long term grazing is likely to impact the canopy through changes in tree population dynamics). Given these assumptions, we would expect that species that forage on bare ground

Table 1. Description of height categories used in the impact-of-grazing model

Height (m)	Description	Strata index
0	Ground (either bare or short grass sward or leaf litter)	1
> 0–1	Grassy/low shrub understorey	2
> 1–5	Shrub/sapling understorey	3
> 5	Subcanopy/canopy	4

and/or short grass would increase as grazing pressure increases, while species that forage in the grass/tussock and shrub layer would decrease as grazing pressure increases and, in the short term, species that forage in the canopy would be unaffected by increasing grazing pressure.

Our model assumes that the susceptibility of bird species j to grazing (sg_j) is a function of the proportion of time that species j feeds on the ground minus the proportion of time species j feeds in the grass/tussock and shrub layers:

$$sg_j = x_{1j} - (x_{2j} + x_{3j}) \quad \text{eqn 1}$$

where x_{1j} is the proportion of time species j forages in strata 1, x_{2j} is the proportion of time species j forages in strata 2 and x_{3j} is the proportion of time species j forages in strata 3 (Table 1). This measure of susceptibility is a number between 1 and -1 that is positive for species that feed predominantly on the ground (0 m) and negative for species that forage predominantly in the understorey (> 0–5 m). We predict that positive values of this measure indicate a propensity to increase in abundance with increasing grazing pressure, while negative values suggest a tendency to decrease in abundance. An average susceptibility to grazing measure was calculated when more than one relevant study reported foraging height data for a particular species.

Methods

STUDY REGION

The study region was located in the south-east Queensland Bioregion, Australia (Sattler & Williams 1999). It is bounded by 26–28°S and 151–153°E and ranges in elevation between 300 and 550 m.a.s.l. The climate is subtropical, with most rain falling in summer and frosts occurring between May and September. Annual rainfall is approximately 960 mm, with a temperature range in

the hottest month (January) averaging 17–28 °C and the coolest month (July) 5–16 °C. Temperatures frequently dropped below freezing across most of the study sites in winter. The dominant soil types are derived from metamorphic, granite, sandstone and alluvium landforms.

The vegetation is grassy eucalypt woodland and forest. In many areas the number and size of trees has been modified during early settlement by ring barking, a process by which trees are killed through the removal of a ring of bark around the stem of the tree. More recently, stem-injection of herbicides into trees has become the major management practice to remove woody overstorey in an effort to maintain grass production. Currently more than one-third of the study region is covered by woodland. The landscape is variegated, with native vegetation comprising the majority of the landscape matrix (60–90%) (McIntyre & Hobbs 1999). The native vegetation has been modified to various degrees by grazing and other disturbances but, overall, intensive land uses such as cropping and sown pasture are limited. The most abundant eucalypts are *Eucalyptus crebra*, *Eucalyptus melanophloia* and, on the lower slopes and within riparian habitats, *Eucalyptus tereticornis* (Martin *et al.* 2000).

SITE SELECTION AND DESCRIPTION

Sites were chosen based on understorey composition and structure using a combination of aerial photos, topography and soil maps, followed by ground truthing. The probable grazing history of a site was ascertained from discussions with landholders on the historical and current stocking rates of their property, knowledge of patch formation dynamics in subtropical grassy woodlands (McIvor *et al.* 2005), the present structural condition of the grass sward and the plant species composition of the sites (McIntyre & Martin 2001, 2002; McIntyre, Heard & Martin 2002, 2003). Three levels of grazing were defined: no/low, moderate and high (Table 2).

Table 2. Description of habitat treatments

Habitat	Grazing level	Treatment (habitat type and grazing level)
Grassy eucalypt woodland sites (W)		
W	1	Grassy eucalypt woodland intact (exclosures, stock routes): no/low grazed; land use indicative of a history of no, little or infrequent grazing; swards intact; native trees, shrubs, grassland present
W	2	Woodland modified (in paddock): moderately grazed; large native tussock grass structure as well as short grazed patches, indicating selective grazing; majority of shrub layer absent
W	3	Woodland modified (in paddock): highly grazed; closely cropped lawn-like understorey structure, dominated by stoloniferous/rhizomatous grasses indicating prolonged non-selective grazing; shrub layer absent
Riparian sites (R)		
R	1	Riparian vegetation intact (exclosures): no/low grazed (as above W1); tree, shrub and herbaceous layer present; surrounded by vegetation consistent with W1
R	2	Riparian vegetation modified (in paddock): moderately grazed (as with W2); surrounded by vegetation, consistent with W2
R	3	Riparian vegetation modified (in paddock): highly grazed (as with W3); surrounded by vegetation consistent with W3

Woodland and riparian habitats representing the grazing treatments (Table 2) were surveyed to determine the potential impact of grazing on the abundance of bird species. Eight replicate sites of each grazing treatment in each habitat (three woodland, three riparian) were selected, giving a total of 48 sites. Each grazing treatment had to be a minimum of 20 ha in extent. Riparian sites were situated within woodlands with a grazing level that corresponded to the sampled riparian site.

Woodland and riparian sites with a uniform tree density across all three grazing regimes were chosen to avoid the grazing effect being confounded by differences in tree density. Survey sites were stratified across an area of 1000 km² and the distance between sites was a minimum of 1 km.

BIRD SAMPLING

Each of the 48 sites contained a 2-ha search area (Barrett *et al.* 2003), where the abundance of all bird species seen or heard was recorded during a 20-min interval on two different days and repeated for each season, giving a total of 192 site visits. With the exception of aerial feeders (swifts, swallows and raptors), all birds flying 20 m or above were excluded.

A single observer completed the surveys. Bird counts were made on fine mornings in summer (November–January 2001–02) between 04.45 and 09.45 h and in winter (June–July 2002) between 06.45 and 11.45 h. Surveys were not conducted during summer, above 35 °C, or during winter when the temperature fell below –2 °C. To avoid possible sampling bias, a restricted random visitation method was used, whereby the entire survey was partitioned into six geographical regions and each region (and subsequent site within each region) was visited randomly (MacNally & Horricks 2002).

COMPARISON OF FIELD DATA WITH IMPACT-OF-GRAZING MODEL

We calculated the change in species abundance as grazing pressure increases (e.g. from no/low to moderate; no/low to high; and moderate to high grazing), referred to as relative change. Bird species abundance across the eight replicate grazing treatments for each habitat, from summer and winter, were combined in order to calculate the relative change in density for each species in each grazing level transition for the woodland and riparian sites, respectively, and density values were standardized between –1 and 1 (see the Appendix).

Let y_{jk} be the density of species j at grazing level k , where k is equal to l for no/low grazed, m for moderate grazed and h for high grazed sites. Therefore the relative change from no/low (l) to high (h) grazing for species j is:

$$lh_j = \frac{y_{jh} - y_{jl}}{y_{jh} + y_{jl}} \quad \text{eqn 2}$$

and lm_j is from no/low to moderate grazing and mh_j is from moderate to high grazing. For example, if species j is present under high ($y_{jh} > 0$) grazing but absent under no/low grazing ($y_{jl} = 0$) then lh_j is equal to 1, whereas if species j is present under no/low grazing ($y_{jl} > 0$) but absent from high grazing ($y_{jh} = 0$) then lh_j is equal to –1. This relative change for each grazing transition is then plotted against the susceptibility to grazing measure.

Spearman's rank correlations were performed to test the strength of the relationship between our predictions from the grazing impacts model and the relative change in density value for each grazing level transition. We were primarily interested in the overall trend rather than an exact fit of the correlation, i.e. do species that are predicted to decline actually decline? If our model is a good predictor of a bird's susceptibility to grazing then we would expect to find most bird species in the upper right quadrant or lower left quadrant shown in Fig. 1. That is, a species predicted to increase is observed to increase, and a species predicted to decline is observed

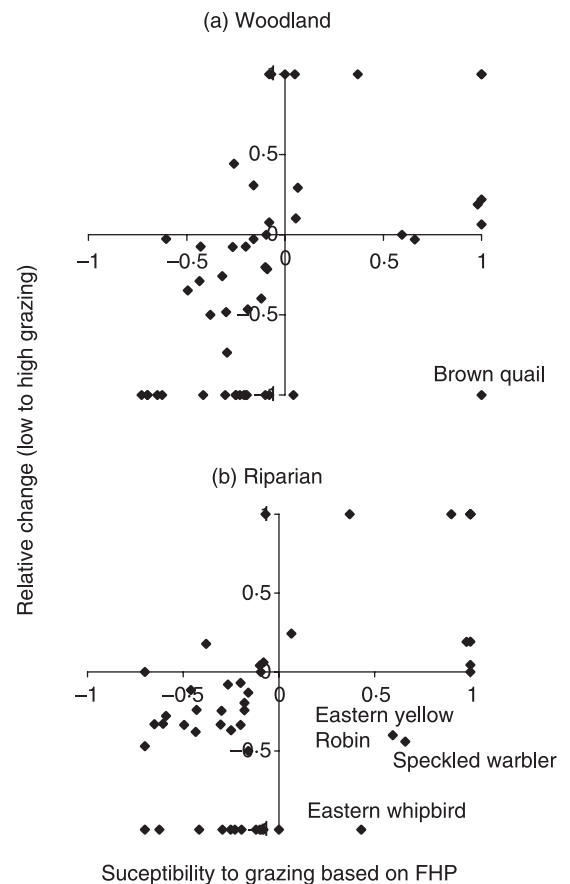


Fig. 1. Plot of susceptibility to grazing based on foraging height preference (FHP) and relative change in abundance from no/low grazing to high grazing for (a) woodland and (b) riparian habitat. Relative change is positive if a species increases in abundance with grazing. If our forage model is a good predictor of a species' response to increased grazing pressure, then we expect the foraging height preference (FHP) plotted against the relative change in abundance to fall in quadrants (–1, –1) and (1, 1), whereas species that do not fit the model will be in (1, 1) and (–1, 1).

to decline. Species that show an opposite response to that predicted would be in either the upper left or lower right quadrant. All analyses were performed using freeware package R (R Development Core Team 2004).

SPECIES INCLUDED

Species included in the analyses were limited by the availability of published data on the proportion of time a species spent foraging at different heights (see the Appendix). In addition, prior to analysis, birds of prey, aerial feeders (e.g. swifts and swallow) and aquatic birds (e.g. ducks, grebes and cormorants) were excluded because foraging for these species occurs primarily away from terrestrial vegetation. Finally, a minimum of two field observations was required in a habitat (riparian, woodland) to be included in the analysis. A list of species, studies used and resulting susceptibility to grazing measure and relative change values for one grazing transition (no/low to high grazing) for woodland and riparian habitat is shown in the Appendix. Nomenclature follows Christidis & Boles (1994).

Results

The susceptibility to grazing measure was a significant predictor of differences in bird density in grazed habitats (Fig. 1 and Tables 3 and 4). In both woodland and

riparian sites, 80% and 78%, respectively, of species' predictions corresponded with the observed change in species' densities from no/low grazing to high grazing (Table 4). While the correlation coefficients were not high they indicated that there was a significant relationship between the predictions from the impact-of-grazing model based on foraging height preference and changes in bird density as grazing intensity increases (Table 3).

Correlations were strongest for both woodland and riparian habitats from no/low to moderate grazing and, the most dramatic change in grazing state, no/low to high grazing. The number of species predicted to decline was three times the number predicted to increase and most woodland birds predicted to decline did, in fact, decline (Fig. 1).

Of the 58 species included in the analyses, 53 were recorded in both woodland and riparian habitats. Four species (azure kingfisher *Alcedo azurea*, eastern whipbird *Psophodes olivaceus*, red-rumped parrot *Psephotus haematonotus*, straw-necked ibis *Threskiornis spinicollis*) were recorded in riparian habitats only and one species (brown quail *Coturnix ypsilophora*) in woodland only.

Thirty-one species were predicted to decline and did decline with increased grazing pressure. These included understorey specialist species (e.g. brown thornbill *Acanthiza pusilla*, variegated fairy-wren *Malurus lamberti* and white-browed scrubwren *Sericornis frontalis*), subcanopy and canopy feeders (e.g. buff-rumped thornbill *Acanthiza reguloides*, fuscous honeyeater *Lichenostomus fuscus*, spotted pardalote *Pardalotus punctatus*, scarlet honeyeater *Myzomela sanguinolenta*, white-throated honeyeater *Melithreptus albogularis* and white-naped honeyeater *Melithreptus lunatus*) and the riparian specialist, azure kingfisher *Alcedo azurea*. Nine species predicted to increase that did increase were ground foragers (e.g. crested pigeon *Ocyphaps lophotes*, masked lapwing *Vanellus miles*, magpie-lark *Grallina cyanoleuca*, straw-necked ibis *Threskiornis spinicollis* and yellow-rumped thornbill *Acanthiza chrysorrhoa*).

Species that did not fit the model well tended to fall close to the edges of quadrants in Fig. 1 rather than at the extremes, and included a group of large-bodied ground foragers (e.g. Australian magpie *Gymnorhina*

Table 3. Results of Spearman's rank correlation (*r*) between the foraging height preference and relative change for woodland and riparian habitats, showing *n* number of pairs and *P*-value

Grazing transitions	Woodland			Riparian		
	<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>
No/low to moderate	0.61	50	< 0.0001	0.50	49	0.0001
Moderate to high	0.57	50	< 0.0001	0.45	50	0.0006
No/low to high	0.36	47	0.009	0.39	48	0.004

Table 4. Summary of a priori predictions and observed relative change in density from no/low to high grazing for both woodland and riparian habitats

Prediction	Relative change	Woodland		Riparian	
		No. species	%	No. species	%
Decrease	Decrease	31	62	29	58
Increase	Increase	9	18	10	20
Decrease	Increase	5	10	4	8
Increase	Decrease	3	6	3	6
Decrease	Zero	1	2	2	4
Zero	Increase		0		0
Zero	Decrease		0	1	2
Increase	Zero	1	2	1	2
Total		50		50	

tibicen, galah *Cacatua roseicapilla* and torresian crow *Corvus orru*). Notable exceptions were a group of small-bodied ground foragers (e.g. brown quail *Coturnix ypsilophora*, eastern whipbird *Psophodes olivaceus*, eastern yellow robin *Eopsaltria australis* and speckled warbler *Chthonicola sagittata*; Fig. 1).

Discussion

Our predictive approach to examining the role of grazing in shaping Australian woodland bird assemblages has demonstrated that foraging height preference is a good predictor of a bird's susceptibility to livestock grazing. There are many reasons why our impact-of-grazing model should fail. First, small sample sizes for some species (e.g. brown thornbill *Acanthiza pusilla* and eastern yellow robin *Eopsaltria australis*) will obscure any prediction. Secondly, there are likely to be many other facets that influence the presence of species other than availability of feeding substrates. Thirdly, grazing affects habitat in more ways than simply altering vegetation structure. However, despite these limitations the impact-of-grazing model successfully predicts changes in bird species abundance.

The strength of the correlation between bird species diversity and habitat structural diversity is tied to the varying availability and exploitation of substrates, food types and other habitat resources (Willson 1974; Karr 1976). At the most simplistic level a species will not be present unless there are appropriate resources for it to use (Ford 1989). Livestock grazing of woodland and riparian habitats alters the vegetation structure by modifying and often removing the understorey vegetation, thereby changing the resources available for birds. Through an understanding of where birds forage in intact, non-grazed vegetation, we successfully predicted whether bird species abundance was likely to increase, decrease or remain unaffected with increasing grazing pressure for the majority of bird species under consideration (Table 4, and see the Appendix).

In this study, loss of understorey vegetation induced by cattle grazing resulted in a decline in abundance of many woodland bird species. At high levels, livestock grazing causes a major structural and plant species shift in the understorey vegetation, where perennial tussock grasses are lost and lawn-forming rhizomatous and stoloniferous grasses predominate (McIvor *et al.* 2005). The bird assemblage also showed a dramatic change, from one dominated by small-bodied woodland species found in no/low grazed woodlands, to an assemblage made up large-bodied 'generalist' species that are increasing nationally (Barrett *et al.* 2003). The patterns under moderate grazing were more complex, with some notable woodland birds (e.g. brown treecreeper *Climacteris picumnus*, speckled warbler *Chthonicola sagittata*, jacky winter *Microeca fascinans* and varied sittella *Daphoenositta chrysoptera*) increasing in abundance or remaining stable. Under moderate levels, large tussock perennial grasses dominated the understorey

and were grazed to varying degrees. This increased structural diversity and may provide new foraging opportunities. Through knowledge of where in the vegetation strata birds forage and the grazing impacts on vegetation structure, we were able to predict correctly changes in abundance of most woodland bird species under consideration. With more than 70% of Australia and significant areas on other continents under livestock grazing, this method could be used widely to help predict which bird species are most at risk from this type of land use.

Our model was designed to detect coarse monotonic trends associated with grazing. However, we know that some species do not respond monotonically (Martin *et al.* 2005). For example, the brown quail was predicted to increase under grazing yet showed an intermediate response, reaching its highest abundance under moderate levels of grazing. In contrast, the dusky woodswallow *Artamus cyanopterus* was predicted to decline with grazing and did decline under high grazing but increased under moderate grazing compared with no/low grazing pressure. Thus, while our model may predict the correct response for one grazing transition, the prediction may be incorrect for another.

Several species that were predicted to increase markedly with increases in grazing, based on their preference for foraging on the ground (e.g. Australian magpie, galah and torresian crow), showed only slight increases in abundance. These species are pervasive throughout grassy woodlands regardless of grazing intensity, therefore the relative change in abundance from one grazing level to another was marginal.

A model that could accommodate the influence of 'substrate type' may have improved predictions for some ground foraging birds (e.g. eastern yellow robin, eastern whipbird and speckled warbler) as these species are known to forage in leaf litter as well as short grass and bare ground (Ford, Noske & Bridges 1986) and grazing is likely to decrease the amount of leaf litter. However, this information is not widely reported; hence it is not clear how it could be accommodated a priori.

Our model could be extended to test the relative importance of seasonality and sex on bird species susceptibility to grazing. Variation in the place and time that resident and migrant insectivores (Recher & Davis 2002) and nectivores (Woinarski, Connors & Franklin 2000) exploit different food resources has been documented for woodland bird fauna. Research has also demonstrated sexual dimorphism in foraging heights (Recher & Holmes 2000).

The method reported here should be useful for informing management decisions relating to landscape restoration, intensification and abandonment. With extensive habitat restoration efforts under way across southern Australia, North America and Europe, pasture abandonment throughout parts of Europe (Blanco, Tella & Torre 1998; Laiolo *et al.* 2004), as well as landscape intensification across many continents, this approach could be used to predict which birds are likely

to utilize different habitats under various management regimes (Raman, Rawat & Johnsingh 1998). It is widely presumed that restoration efforts will benefit biodiversity, but there is little general theory to guide restoration efforts (Hobbs & Norton 1996). This modelling approach could be adapted to predict when habitat resources (food and nest sites) for birds or other fauna are likely to become available or, conversely, when they are likely to disappear. Simulating the growth or removal of different vegetation layers and features (e.g. hollows and fruit set) would provide a habitat trajectory over time. Knowledge of foraging height preference or nesting requirements could then be used to predict when an evolving habitat would become suitable for colonization.

CONCLUSION

Ecologists and resource managers need a sound basis upon which to make management decisions; for conservation biology and ecology to mature as disciplines we must go beyond case-by-case interpretation and be able to predict with confidence the impacts of different land uses in a range of environment (Peters 1991; MacNally & Bennett 1997). In order to achieve this we must pose hypotheses with testable predictions (MacNally & Bennett 1997; MacNally, Bennett & Horricks 2000), as without these we have no way to forecast (Peters 1991). Ecologists must consider the mechanisms underlying change rather than search for patterns to infer change. The ability to forecast which species are most vulnerable to grazing by livestock would facilitate a proactive approach to the management of habitats at the landscape, regional and continental scales. The method reported here has allowed us to demonstrate that most woodland and riparian birds decline with increasing grazing pressure and, most importantly, their preferred foraging height is a significant determinant of their susceptibility to livestock grazing. This approach can be applied to other areas where landscapes are in a state of transition, to provide crucial information on which to make conservation management decisions.

Acknowledgements

We thank the Copley, Irwin, Kerr, McConnell, McCrae, Parton, Patch, Serensen, Rowlings, Tickle and Wright families for providing access to their properties and for their support of this project. Special thanks to Bob Wright and Susi Serensen for providing accommodation for the duration of this study. This paper has benefited from discussions with Henrik Andrén, Sue McIntyre and Thomas Sisk and members of The Spatial Ecology Laboratory, University of Queensland, and helpful comments from Amy Jansen. Thank you to CSIRO Sustainable Ecosystems Rangeland and Savannas Program for supporting this project logistically and financially. In addition, this project was supported financially by a Birds Queensland Research Award, Birds Australia, Stuart Leslie Research

Award, and an Australian Postgraduate Award to T. Martin.

Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE1012/JPE1012sm.htm>.

Appendix. Mean abundance and standard deviation for 58 species across the three grazing levels

References

- Abensberg-Traun, M. & Smith, G.T. (1993) Predictable effects of agricultural development on the long-term availability of hollows for animals: observations from the western Australian wheatbelt. *Pacific Conservation Biology*, **1**, 78–79.
- Abensberg-Traun, M., Smith, G.T., Arnold, G.W. & Steven, D.E. (1996) The effects of habitat fragmentation and livestock-grazing on animal communities in remnants of gimlet *Eucalyptus salubris* woodland in the western Australian wheatbelt. I. Arthropods. *Journal of Applied Ecology*, **33**, 1281–1301.
- Arnold, G.W. & Weeldenburg, J.R. (1998) The effects of isolation, habitat fragmentation and degradation by livestock grazing on the use by birds of patches of gimlet *Eucalyptus salubris* woodland in the wheatbelt of western Australia. *Pacific Conservation Biology*, **4**, 155–163.
- Barrett, G., Silcocks, A., Barry, S., Cunningham, R. & Poulter, R. (2003) *The New Atlas of Australian Birds* Royal Australasian Ornithologists' Union, Victoria, Australia.
- Bell, H.L. (1985) The social organization and foraging behaviour of three syntopic thornbills *Acanthiza* spp. *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management* (eds A. Keast, H.F. Recher, H. Ford & D. Saunders), pp. 151–163. Royal Australasian Ornithologists' Union and Surrey Beatty & Son, Chipping Norton, Australia.
- Bell, S.S., McCoy, E.D. & Mushinsky, H.R. (1991) *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London, UK.
- Blanco, G., Tella, J.L. & Torre, I. (1998) Traditional farming and key foraging habitats for chough *Pyrrhocorax pyrrhocorax* conservation in a Spanish pseudosteppe landscape. *Journal of Applied Ecology*, **35**, 232–239.
- Brooker, M.G., Braithwaite, R.W. & Estberg, J.A. (1990) Foraging ecology of some insectivorous and nectivorous species of birds in forests and woodlands of the wet-dry tropics of Australia. *Emu*, **90**, 215–230.
- Chan, K. (1990) Habitat selection in the white-plumed honeyeater and the fuscous honeyeater at an area of sympatry. *Australian Journal of Ecology*, **15**, 207–217.
- Christidis, L. & Boles, W.E. (1994) *The Taxonomy and Species of Birds of Australia and its Territories*. RAOU, Melbourne, Australia.
- Cody, M.L. (1968) On the methods of resource division in grassland bird communities. *American Naturalist*, **102**, 107–147.
- Cody, M.L. (1974) *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton, NJ.
- Dambach, C.A. (1944) A ten-year ecological study of adjoining grazed and ungrazed woodlands in northeastern Ohio. *Ecological Monographs*, **14**, 255–270.
- Dambach, C.A. & Good, E.E. (1940) The effect of certain land use practices on populations of breeding birds in southwestern Ohio. *Journal of Wildlife Management*, **4**, 63–76.

- Fensham, R.J. & Skull, S.D. (1999) Before cattle: a comparative floristic study of eucalyptus savanna grazed by macropods and cattle in north Queensland, Australia. *Biotropica*, **31**, 37–47.
- Ford, H.A. (1989) *Ecology of Birds: An Australian Perspective*. Surrey Beatty & Sons Pty Ltd, Chipping Norton, Australia.
- Ford, H.A. & Paton, D.C. (1976) Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. *Australian Journal of Ecology*, **1**, 281–287.
- Ford, H.A., Noske, S. & Bridges, L. (1986) Foraging of birds in eucalypt woodland in north-eastern New South Wales. *Emu*, **86**, 168–179.
- Frith, D.W. (1984) Foraging ecology of birds in an upland tropical rainforest in North Queensland. *Australian Wildlife Research*, **11**, 325–347.
- Frith, H.J. (1976) *Complete Book of Australian Birds*. Readers Digest Services Pty Ltd, Sydney, Australia.
- Garnett, S.T. & Crowley, G.M. (2000) *The Action Plan for Australian Birds 2000*. Environment Australia, Canberra, Australia.
- Good, E.E. & Dambach, C.A. (1943) Effect of land use practices on breeding bird populations in Ohio. *Journal of Wildlife Management*, **7**, 291–297.
- Haila, Y., Järvinen, O. & Väisänen, R.A. (1980) Effects of changing forest structure on long-term trends in bird populations in SW Finland. *Ornis Scandinavica*, **11**, 12–22.
- Hartley, P.H.T. (1953) An ecological study of the feeding habitats of the English titmouse. *Journal of Animal Ecology*, **22**, 261–288.
- Higgins, P.J. (1999) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 4. Parrots to Dollarbirds*. Oxford University Press, Melbourne, Australia.
- Higgins, P.J. & Davies, S.J.J.F. (1996) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 3. Snipe to Pigeons*. Oxford University Press, Melbourne, Australia.
- Higgins, P.J. & Peter, J.M. (2002) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 6. Pardalotes to Shrike-Thrushes*. Oxford University Press, Melbourne, Australia.
- Higgins, P.J., Peter, J.M. & Steele, W.K. (2001) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 5. Tyrant-Flycatchers to Chats*. Oxford University Press, Melbourne, Australia.
- Hobbs, R.J. & Norton, D.A. (1996) Towards a conceptual framework for restoration ecology. *Restoration Ecology*, **4**, 93–110.
- James, C.D. (2003) Responses of vertebrates to fence-line contrasts in grazing intensity in semi-arid woodlands of eastern Australia. *Austral Ecology*, **28**, 137–151.
- Jansen, A. & Robertson, A.I. (2001) Relationships between livestock management and the ecological condition of riparian habitats along an Australian floodplain river. *Journal of Applied Ecology*, **38**, 63–75.
- Jansen, R., Little, R.M. & Crowe, T.M. (1999) Implications of grazing and burning of grasslands on the sustainable use of francolins (*Francolinus* spp.) and on overall bird conservation in the highlands of Mpumalanga province, South Africa. *Biodiversity and Conservation*, **8**, 587–602.
- Karr, J.R. (1976) Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist*, **110**, 973–994.
- Kauffman, J.B. & Krueger, W.C. (1984) Livestock impacts on riparian ecosystems and streamside management implications. A review. *Journal of Range Management*, **37**, 430–438.
- Knopf, F.L., Sedwick, J.A. & Cannon, R.W. (1988) Guild structure of a riparian avifauna relative to seasonal grazing. *Journal of Wildlife Management*, **52**, 280–290.
- Krueger, D., Bart, J. & Rich, T.D. (2003) Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona (USA). *Conservation Biology*, **17**, 607–615.
- Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, **41**, 294–304.
- Ludwig, J.A., Eager, R.W., Liedloff, A.C., McCosker, J.C., Hannah, D., Thurgate, N.Y., Woinarski, J.C.Z. & Catterall, C.P. (2000) Clearing and grazing impacts on vegetation patch structure and fauna counts in eucalypt woodland, Central Queensland. *Pacific Conservation Biology*, **6**, 254–272.
- MacArthur, R.H. (1958) Population ecology of some warblers on northeastern coniferous forests. *Ecology*, **39**, 599–619.
- MacArthur, R.H. (1964) Environmental factors affecting bird species diversity. *American Naturalist*, **98**, 387–397.
- MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, **42**, 594–598.
- MacArthur, R.H., Recher, H.F. & Cody, M. (1966) On the relation between habitat selection and species diversity. *American Naturalist*, **100**, 319–332.
- McIntyre, S. & Hobbs, R.J. (1999) A framework for conceptualizing human impacts on landscapes and its relevance to management and research models. *Conservation Biology*, **13**, 1282–1292.
- McIntyre, S. & Martin, T.G. (2001) Biophysical and human influences on plant species richness in grasslands: comparing variegated landscapes in subtropical and temperate regions. *Austral Ecology*, **26**, 233–245.
- McIntyre, S. & Martin, T.G. (2002) Managing intensive and extensive land uses to conserve grassland plants in subtropical eucalypt woodlands. *Biological Conservation*, **107**, 241–252.
- McIntyre, S., Heard, K.M. & Martin, T.G. (2002) How grassland plants are distributed over five human-created habitats typical of eucalypt woodlands in a variegated landscape. *Pacific Conservation Biology*, **7**, 274–289.
- McIntyre, S., Heard, K.M. & Martin, T.G. (2003) The relative importance of cattle grazing in sub-tropical grasslands: does it reduce or enhance plant biodiversity? *Journal of Applied Ecology*, **40**, 445–457.
- McIvor, J.G., McIntyre, S.M., Saeli, I. & Hodgkinson, J.J. (2005) Patch dynamics in grazed sub-tropical native pastures in south-east Queensland. *Austral Ecology*, in press.
- MacNally, R.C. (1990) The roles of floristics and physiognomy in avian community composition. *Australian Journal of Ecology*, **15**, 321–327.
- MacNally, R. & Bennett, A.F. (1997) Species-specific predictions of the impact of habitat fragmentation: local extinction of birds in the box-ironbox forests of central Victoria, Australia. *Biological Conservation*, **82**, 147–155.
- MacNally, R. & Horricks, G. (2002) Relative influences of patch, landscape and historical factors on birds in a fragmented landscape. *Journal of Biogeography*, **29**, 395–410.
- MacNally, R., Bennett, A.F. & Horricks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box-ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7–29.
- MacNally, R., Parkinson, A., Horricks, G., Conole, L. & Tzaros, C. (2001) Relationships between terrestrial vertebrate diversity abundance and availability of coarse woody debris on south-eastern Australian floodplains. *Biological Conservation*, **99**, 191–205.
- Marchant, S. & Higgins, P.J. (1990) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 1. Ratites to Ducks, Part B Australian Pelican to Ducks*. Oxford University Press, Melbourne, Australia.
- Marchant, S. & Higgins, P.J. (1993) *Handbook of Australian, New Zealand and Antarctic Birds. Volume 2. Raptors to Lapwings*. Oxford University Press, Melbourne, Australia.
- Martin, T.G. & Green, J.G. (2002) Wildlife and core conservation areas. *Managing and Conserving Grassy Woodlands*

- (eds S. McIntyre, J.G. McIvor & K.M. Heard), pp. 111–142. CSIRO Publishing, Melbourne, Australia.
- Martin, T.G., Best, K.M., McIntyre, S., McIvor, J.G. & MacLeod, N.D. (2000) *Four Grazing Properties in South-east Queensland: Pattern of Land Use and Ecological Status*. Technical Memorandum No. 5. CSIRO Tropical Agriculture, Brisbane, Australia.
- Martin, T.G., Kuhnert, P.M., Mengersen, K. & Possingham, H.P. (2005) The power of expert opinion in ecological models: a Bayesian approach examining the impact of livestock grazing on birds. *Ecological Applications*, **15**, 266–280.
- Peters, R.H. (1991) *A Critique for Ecology*. Cambridge University Press, Cambridge.
- Popotnik, G.J. & Guiliano, W.M. (2000) Response of birds to grazing of riparian zones. *Journal of Wildlife Management*, **64**, 976–982.
- R Development Core Team (2004) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Recher, H.F. (1969) Bird species diversity and habitat diversity in Australia and North America. *American Naturalist*, **103**, 75–80.
- Recher, H.F. (1991) The conservation and management of eucalypt forests birds: resource requirements for nesting and foraging. *Conservation of Australia's Forest Fauna* (ed. D. Lunney), pp. 25–34. Royal Zoological Society of NSW, Mosman, Australia.
- Recher, H.F. (1999) The state of Australia's avifauna: a personal opinion and prediction for the new millennium. *Australian Zoologist*, **31**, 11–27.
- Recher, H.F. & Davis, W. (1998) The foraging profile of a wandoo woodland avifauna in early spring. *Australian Journal of Ecology*, **23**, 514–527.
- Recher, H.F. & Davis, W.E. (2002) Foraging profile of a salmon gum woodland avifauna in western Australia. *Journal of Royal Society of Western Australia*, **85**, 103–111.
- Recher, H.F. & Holmes, R.T. (2000) The foraging ecology of birds of eucalypt forest and woodland. I. Differences between males and females. *Emu*, **100**, 205–215.
- Recher, H.F., Holmes, R.T., Schultz, M., Shields, J. & Kavanagh, R. (1985) Foraging patterns of breeding birds in eucalypt forest and woodland of southeastern Australia. *Australian Journal of Ecology*, **10**, 399–419.
- Rice, J., Anderson, B.W. & Ohmart, R.D. (1984) Comparison of the importance of different habitat attributes to avian community organization. *Journal of Wildlife Management*, **48**, 895–911.
- Sattler, P.S. & Williams, R.D.E. (1999) *The Conservation Status of Queensland's Bioregional Ecosystems*. Environmental Protection Agency, Brisbane, Australia.
- Sedgwick, J.A. & Knopf, F.L. (1987) Breeding bird response to cattle grazing of a cottonwood bottomland. *Journal of Wildlife Management*, **51**, 230–237.
- Shankar Raman, T.R., Rawat, G.S. & Johnsingh, A.J.T. (1998) Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology*, **35**, 214–231.
- Soderstrom, B., Part, T. & Linnarsson, E. (2001) Grazing effects on between-year variation of farmland bird communities. *Ecological Applications*, **11**, 1141–1150.
- Stanley, T.R. & Knopf, F.L. (2002) Avian responses to late-season grazing in a shrub-willow floodplain. *Conservation Biology*, **16**, 225–231.
- Tibbetts, E. & Pruett-Jones, S. (1999) Habitat and nest-site partitioning in splendid and variegated fairy-wrens (Aves: Maluridae). *Australian Journal of Zoology*, **47**, 317–326.
- Tidemann, S.C. (1983) *The behavioural ecology of three coexisting fairy-wrens (Maluridae: Malurus)*. PhD Thesis. Australian National University, Canberra, Australia.
- Traill, B.J. & Duncan, S. (2000) *Status of Birds in the New South Wales Temperate Woodlands Region*. Consultancy Report to the NSW National Parks and Wildlife Service. Australian Woodlands Conservancy, Victoria, Australia.
- Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K. (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology*, **38**, 647–664.
- Willson, M.F. (1974) Avian community organization and habitat structure. *Ecology*, **55**, 1017–1029.
- Woinarski, J.C.Z. & Ash, A.J. (2002) Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. *Austral Ecology*, **27**, 311–323.
- Woinarski, J.C.Z. & Catterall, C.P. (2004) Historical changes in the bird fauna at Coomooboolaroo, northern Australia, from the early years of pastoral settlement (1873) to 1999. *Biological Conservation*, **116**, 379–401.
- Woinarski, J.C.Z., Connors, G. & Franklin, D.C. (2000) Thinking honeyeater: nectar maps for the Northern Territory, Australia. *Pacific Conservation Biology*, **6**, 61–80.
- Woinarski, J.C.Z., Tidemann, S.C. & Kerin, S. (1988) Birds in a tropical mosaic: the distribution of bird species in relation to vegetation patterns. *Australian Wildlife Research*, **15**, 171–196.

Received 30 June 2004; final copy received 20 December 2004