THE POWER OF EXPERT OPINION IN ECOLOGICAL MODELS USING BAYESIAN METHODS: IMPACT OF GRAZING ON BIRDS

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Abstract. One of our greatest challenges as researchers is predicting impacts of land use on biota, and predicting the impact of livestock grazing on birds is no exception. Insufficient data and poor survey design often yield results that are not statistically significant or difficult to interpret because researchers cannot disentangle the effects of grazing from other disturbances. This has resulted in few publications on the impact of grazing on birds alone.

Ecologists with extensive experience in bird ecology in grazed landscapes could inform an analysis when time and monetary constraints limit the amount of data that can be collected. Using responses from 20 well-recognized ecologists throughout Australia, we captured this expert knowledge and incorporated it into a statistical model using Bayesian methods. Although relatively new to ecology, Bayesian methods allow straightforward probability statements to be made about specific models or scenarios and the integration of different types of information, including scientific judgment, while formally accommodating and incorporating the uncertainty in the information provided.

Data on bird density was collected across three broad levels of grazing (no/low, moderate, and high) typical of subtropical Australia. This field data was used in conjunction with expert data to produce estimates of species persistence under grazing. The addition of expert data through priors in our model strengthened results under at least one grazing level for all but one bird species examined. When experts were in agreement credible intervals were tightened substantially, whereas, when experts were in disagreement, results were similar to those evaluated in the absence of expert information. In fields where there is extensive expert knowledge, yet little published data, the use of expert information as priors for ecological models is a cost effective way of making more confident predictions about the effect of management on biodiversity.

Key words: elicitation; false negative error; livestock grazing; Markov Chain Monte Carlo; mixture model; multiple experts; two-component model; WinBUGS; woodland bird conservation; zero-inflation.

Introduction

Livestock grazing affects more land in Australia, and on most continents, than any other form of land use (NLWA 2002). While a great deal of research on bird abundance has focused on the removal of woody vegetation, little has considered the impact of grazing on the understorey in the absence of changes in the tree layer (e.g., Sedgwick and Knopf 1987, Woinarski and Ash 2002, James 2003). One of the challenges with determining the subtle impacts of grazing on highly variable measures like bird abundance is lack of power (Toft and Shea 1983, Osenberg et al. 1994).

The process of eliciting information from experts and incorporating it into models to enhance their explanatory and predictive power is a topic of ongoing interest (Kadane and Wolfson 1998, O'Hagan 1998). In ecol-

ogy, the Delphi method (Delbecq et al. 1975) and its variants is frequently applied (e.g., McIntyre et al. 2000). Recently, expert knowledge has been used in habitat modeling (Pearce et al. 2001, Yamada et al. 2003), landscape planning (Lawrence et al. 1997, Kangas et al. 2000, Musacchio and Coulson 2001), and to characterize areas of (dis)agreement in plant response to disturbance (Iglesias and Kothmann 1998). Expert judgment is used in these studies through summary statistics describing trends across different scenarios.

While Bayesian methods are gaining use in ecology and conservation biology (e.g., Gazey and Staley 1986, McCarthy et al. 2001, Mac Nally et al. 2002, O'Hara et al. 2002, Dorazio and Johnson 2003), elicitation and models that incorporate expert information through priors have been underutilized (Carpenter 2002). One exception is the work by Crome et al. (1996), which demonstrates how expert beliefs on the effects of logging could be incorporated as informative priors in a Bayesian model to assess the impacts on birds and mammals.

Solving inference and decision-making problems under conditions of uncertainty is integral to ecological

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TABLE 1. Three treatment levels of grazing examined.

No.	Grazing intensity	Location	Description
1	low/no grazing	exclosures, stock routes	land use indicative of a history of no, little, or infrequent grazing; grass swards are intact
2	moderate grazing	pasture	large tussock grass structure present, indicating selective grazing
3	high grazing	pasture	closely cropped, lawn-like areas indicating nonselective grazing

modeling. Bayesian inference can accommodate uncertainty from all stages of modeling and decision making (Ghazoul and McAllister 2003, Marin et al. 2003). Through Bayesian modeling, straightforward probability statements can be made about specific models or scenarios and they allow the integration of different types of information from a variety of sources, reflecting scientific judgment as well as existing empirical data (Ellison 1996, Ghazoul and McAllister 2003).

In contrast, the interpretation of frequentist null hypothesis testing requires complicated logic, resulting in regular misinterpretation of the results and generating debate over its use (Carver 1978, Dennis 1996, Ludwig 1996, Germano 1999, Johnson 1999, Wade 2000). Furthermore, expert information cannot be easily accommodated formally in the frequentist framework.

This paper has two purposes: First, to examine the impact of grazing on birds in the absence of tree cover change, and, second, to investigate the role of expert opinion to increase statistical power for an ecological question. We show how expert information can be used to inform ecological models using a Bayesian framework, where information is elicited from multiple experts and used in conjunction with field data to enhance the explanatory and predictive power of a model. In doing so, we address three specific questions: (1) How much do expert and field data agree with each other with regard to the impact of cattle grazing on birds? (2) Does the addition of expert information improve model predictions? (3) Under what circumstances do predictions improve?

Several different modeling approaches were assessed during this study and are described in Kuhnert et al. (2004). Whereas the focus of that paper is on the interpretation and implications of using zero-inflated Poisson and Negative Binomial models, this paper focuses on the results of one modeling approach, its ecological interpretation, and the implications of incorporating expert opinion data using Bayesian inference.

If ecologists have to prove everything in every place, then progress will be slow. Here, we are interested in the impact of grazing intensity on woodland birds. Rather than ignoring the wealth of existing knowledge, we have chosen to use expert knowledge to moderate our statistical tests and help determine whether general patterns may hold across the entire continent.

METHODS

Study location

The study region is in the Southeast Queensland Bioregion, Australia (Sattler and Williams 1999), bounded by 26°–28° S and 151°–153° E with an elevation range of 300–550 m. The climate is subtropical with most rain falling between December and March, and frosts occurring between May and September. Annual rainfall is ~960 mm with a temperature range in the hottest month (January) averaging 17°–28°C and the coolest month (July) averaging 5°–16°C. Temperatures drop frequently below freezing across most of the study sites between June and August. The dominant lithologies are metamorphic, granite, sandstone, and alluvium.

The vegetation is grassy eucalypt woodland and forest. In many areas, the density of trees has been modified by ringbarking during early settlement by Europeans. More recently, stem-injection of herbicides into trees has become the major management practice to reduce tree density and maintain grass production. Currently, half to one-third of the region is wooded. The landscape state is variegated, that is, native vegetation comprises the majority of the landscape matrix (60–90%; McIntyre and Hobbs 1999). The native vegetation may be 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 the ironbarks *Eucalyptus crebra*, *E. melanophloia*, and, on the lower slopes, the gum *E. tereticornis* (Martin et al. 2000).

Survey design

Woodland habitats with three types of grazing regimes (Table 1) were surveyed to determine the potential impact of grazing on the presence/absence and abundance of bird species. Eight replicate sites of each grazing regime were sampled, giving a total of 24 sites, visited on two separate days and over two seasons, summer and winter. Woodland 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.

While grazing is a complex disturbance and can have many impacts (Fleischner 1994, Brown and McDonald 1995, Fensham and Skull 1999, McIntyre et al. 2003),

our primary interest was with the effect of grazing on understorey composition and structure and how this then influences bird presence/absence and abundance. Therefore, sites were chosen based on these vegetation characteristics, using a combination of aerial photos, topography, and soil maps, followed by ground truthing. We ascertained the likely grazing history of a site based on plant species composition (McIntyre and Martin 2001, 2002, McIntyre et al. 2002*a*, 2003). This assessment, as well as discussions with landholders on the grazing history of their property combined with the present structural condition of the grass sward, was used to define our treatment, representing three levels of grazing: no/low, moderate, and high grazing (Table 1).

Bird sampling

The 2-ha search area methodology endorsed by the Australian Bird Atlas (Barrett et al. 2003) was adopted for this study. Within 24 survey sites, a 2-ha search area was located within a minimum of 20 ha of the same grazing regime, where counts of bird species were recorded by a single observer during a 20-min interval on two different days and repeated for each season. The observer was not restricted to a transect, but was free to move throughout the 2 ha in search of birds until the site has been covered or the 20 min had elapsed. Notes on the direction in which birds were moving within the site were taken to minimize the chance of recording the same bird(s) twice. Our counts provided an index of abundance for each bird species at each site in each season. All birds flying 20 m above the site were excluded with the exception of aerial feeders: swifts, swallows, and raptors.

Survey sites were stratified across an area of 1000 km^2. In order to minimize the influence of landscape context (e.g., Lindenmayer et al. 1999, Lichstein et al. 2002) and bird movement between sites, sites of the same grazing treatment were situated a minimum of 1 km and, on average, 13 km apart, whereas sites of different grazing treatments were situated a minimum of 10 km and, on average, 22 km apart. As with all observational studies, we cannot guarantee that we have not counted the same bird twice within two different study sites. However, the minimum distances set between sites and the restricted random visitation method adopted (Mac Nally and Horricks 2002), whereby the entire survey region was partitioned into six geographical groups and each region and subsequent sites were visited randomly within that region, minimized this risk.

A single observer, T. G. Martin, with over 10 years experience surveying birds in the region, completed surveys. Bird counts were made on fine mornings in summer (November 2001–January 2002) between 04:45 and 09:45, and in winter (June–July 2002) between 06:45 and 11:45. During summer, surveys were not conducted when the temperature rose above 35°C or during winter below −2°C.

It is possible that the probability of detecting a bird varies with habitat, and in this case, grazing level, and is one of the reasons indices of abundance have been criticized (e.g., Burnham 1981, Rosenstock et al. 2002). We assume that the open structure of grassy eucalypt woodlands, sparse shrub layer (McIntyre et al. 2002*b*), standardizing of tree density across treatments, and the high number of records based on calls rather than sightings in this study minimize the chance of this affecting our data and resulting conclusions. That is, we assume that the chance of detecting a Noisy Miner or Eastern Yellow Robin in a no/low grazed habitat is similar to the chance of detecting them in a high grazed habitat given they are, in fact, present in both habitats. It is also likely that different birds have different detection rates due to their behavior; however, we feel this bias is equal across treatments.

Eliciting priors from the expert

Thirty-two experts with extensive experience in the response of birds to disturbance and field experience in grazed landscapes were invited to participate in the study. They were asked to score how they thought 31 woodland bird species would respond to cattle grazing (see survey in Appendix A). The 31 bird species were chosen based on a pre-survey reconnaissance of the study region where we piloted our bird survey method.

The survey required the expert to give each bird species a positive ($+1$), negative (-1), or zero (0) score depending on whether they thought the abundance of a species was likely to increase, decrease, or remain constant under each level of grazing defined in Table 1. Experts were asked to fill in responses only for species and grazing levels where they were confident of the response. Of the 32 experts contacted, all agreed to complete the survey; however, only 20 experts returned surveys, resulting in a 60% response rate. Experts who took part in the study are listed in the *Acknowledgments*. Up to three reminders via e-mail and phone were given to experts to complete and return the survey.

There has been considerable debate in the statistical literature regarding elicitation methods and how they can be used to form prior distributions and inform analyses (see Kuhnert et al. 2004). Methods of combining information from multiple experts have also generated much discussion (Genest and Zidek 1986, Jacobs 1995). We took a novel approach to the construction of the prior for the random effects model that was used to model the variation between and within grazing levels. The approach used an unweighted average to determine the mean response elicited from the experts, and its precision. The precision represents the inverse of the variance and provides a measure of similarity of the experts' responses.
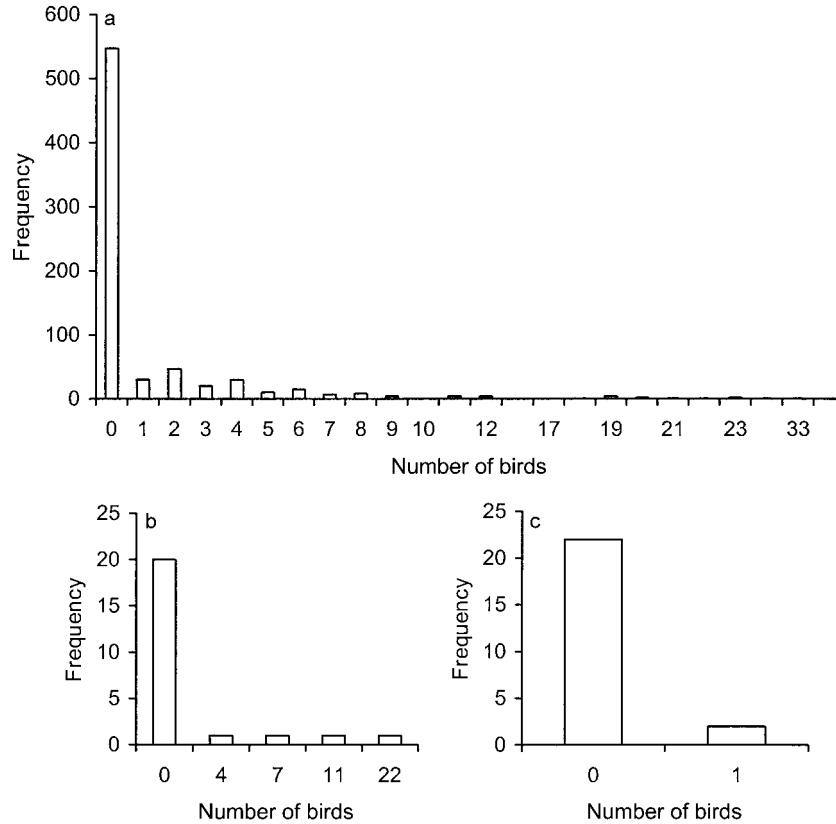
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FIG. 1.   Frequency of bird counts recorded in (a) the entire survey (31 species across eight sites and three treatments, n = 744), (b) Brown Thornbill, (eight sites by three treatments, n = 24), and (c) Rose Robin (n = 24). Note the large number of zero values.

By taking an unweighted average, we avoided difficulties concerned with rating the comparative ''accuracy'' of each expert's opinion about birds and grazing (Einhorn et al. 1977). To some extent, the experts' ability to provide this measure is contained within the expert data, since experts only provided responses to birds for which they were confident.

The Bayesian model

Modeling the number of individual species, y_{ij}, at the ith grazing level for the jth species, may be achieved in a generalized linear modeling framework (McCulloch and Nelder 1989). In these applications, the mean, λ_{ij}, is modeled through an outcome of observed counts, given a set of random effects that describe the variability between species, grazing regimes, and between species within a specific grazing regime.

Discrete distributions such as the Poisson and Negative Binomial are natural choices for modeling count data, and they have been used in numerous applications to model counts of animals or plants (Frome et al. 1973, Lawless 1987, McCullagh and Nelder 1989, Venables and Ripley 1999, Dobson 2002). The latter distribution is appropriate for modeling overdispersion, where there is extra Poisson variation (e.g., induced by large counts

such as flocking birds). However, as Welsh et al. (1996, 2000), and Kuhnert et al. (2004) show, these discrete distributions are not always appropriate, especially if the species has a low frequency of occurrence resulting in a data set with a high frequency of zeros.

The data collected for this study exhibits many more zeros than can be expected by either a Poisson or Negative Binomial distribution as illustrated for all species and two representative species in Fig. 1.

A high frequency of zero values can arise in three ways. A strong seasonal or grazing effect will result in sites with no birds present in one season or particular grazing level. These are structural zeros resulting from a true ecological effect. Random zeros arise in different ways. Visiting a site and not recording a species when it is in fact present gives rise to false negative errors. These occur either as a result of the study, that is, the species occurs but it is not present in the survey period, or alternatively, as a result of the observer failing to detect the bird when it is actually there.

Modeling of data with a high frequency of zero values with a Poisson distribution can lead to spurious results if not somehow accounted for (Kuhnert et al. 2004). Under these conditions, the variance estimates may be seriously underestimated, leading to an over-

statement of the certainty of estimated means and poor identification of the species, grazing, and interaction effects.

There are several different methods for modeling the relationship between habitat variables and abundance where there are many zero counts (Welsh et al. 1996, 2000, Dobbie 2001, Kuhnert et al. 2004).

Following Welsh et al. (1996), counts of a species are modeled as having two states: a state in which a species is present at a site, and a state in which species occur with varying levels of abundance. This is known as a conditional or two-component model, since we model state one, that is, whether any birds occur at a site during the survey and conditional on a bird being present, abundance is modeled by a truncated discrete distribution such as the truncated Poisson or truncated Negative Binomial distribution.

An alternative approach that accommodates the high frequency of zero counts is a mixture model (Lambert 1992). Theoretically, a mixture model should account for both structural and random zeros, where counts arise from a mixture of a point mass at zero and a Poisson distribution (or Negative Binomial) with an unknown probability assigned to each component and unknown parameters for each component (Lambert 1992, Welsh et al. 1996, Kuhnert et al. 2004). Using this approach, we model the probability that a zero is modeled through a Poisson distribution or alternatively as a random zero. The mean number of birds at a site is then estimated given the zeros are modeled in this way. In a mixture model, the parameters relate jointly to the probability of finding an animal and to the abundance, whereas for the two-component model, the parameters can be examined separately, aiding interpretation.

In this paper, we used a two-component approach for modeling our bird data at the site level. As discussed by Kuhnert et al. (2004), this model provided the best fit to the data in terms of the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002) and corresponding residual plots. Furthermore, there was no strong evidence for overdispersion, so we fit a truncated Poisson distribution to the non-zero counts.

The decision to treat factors in the model as random rather than fixed effects was based on the factors under consideration. The grazing levels examined were assumed to be drawn from an infinitely large population of levels and were therefore treated as random effects, whereas a fixed effect is a defined class and comprises all possible levels (e.g., age, sex). Since the experts' response reflected a shift in the mean abundance (increase, decrease, no change), the focus was on the variability in the abundance of each bird species that could be attributed to a particular grazing level rather than the impact of a fixed effect on the mean bird abundance.

In Eq. 1, we model the counts y_{ij} for the ith species under the jth grazing level, where s_{0i} and s_{1i} represent the species random effects for the presence/absence and abundance components, respectively; g_{0j} and g_{1j} represent grazing random effect for the jth grazing level; and the component investigating the variability of species within a grazing level is expressed by sg_{0ij} and sg_{1ij} for each model, respectively. This model can be fit as two separate models, a logistic regression model that models the presence or absence of bird species, z_{ij} (presence/absence component) and a truncated Poisson distribution that models the abundance of birds given presence, $y_{ij}|z_{ij}$ (abundance given presence component).

The Model for presence/absence is $z_{ij} \sim$ Bernoulli(p_{ij}) where

$$z_{ij} = \begin{cases} 1 & \text{if } y_{ij} > 0 \\ 0 & \text{otherwise,} \end{cases}$$

with logit link to random effects

$$\text{logit}(p_{ij}) = s_{0i} + g_{0j} + sg_{0ij}. \qquad (1)$$

The model for abundance conditional on presence is $y_{ij}|z_{ij} = 1 \sim$ truncated Poisson (λ_{ij}) with long link to random effects

$$\log(\lambda_{ij}) = s_{1i} + g_{1j} + sg_{1ij}.$$

Random effects are distributed Normally as

$$s_{c_i} \sim N(0, \tau_{s_c}) \qquad c = 0, 1.; \qquad i = 1, \ldots, 31.,$$

$$g_{c_j} \sim N(0, \tau_{g_c}) \qquad c = 0, 1.; \qquad j = 1, 2, 3.,$$

$$sg_{c_{ij}} \sim N(0, \tau_{sg_c}) \qquad c = 0, 1.; \qquad i = 1, \ldots, 31.;$$
$$j = 1, 2, 3.,$$

with Gamma priors on the precisions of the variance components

$$\tau_{s_c}, \tau_{g_c}, \tau_{sg_c} \sim \text{Ga}(0.1, 0.1) \qquad c = 0, 1,$$

and the variance for both models defined as

$$\sigma^2_{s_c} = 1/\tau_{s_c}; \qquad \sigma^2_{g_c} = 1/\tau_{g_c}; \qquad \sigma^2_{sg_c} = 1/\tau_{sg_c}, \qquad c = 0, 1.$$

Note that here we could have placed a mean (μ) on each random effect (with a corresponding uninformative prior), but with no prior information this mean is set at zero. Each random effect is therefore assigned a non-informative Normal prior with zero mean and corresponding precisions τ_{s_c}, τ_{g_c}, and $\tau_{sg_c}(c = 0, 1)$ for the species, grazing, and interaction term, respectively. The priors for the precision terms are Gamma distributed, with parameters that reflect our lack of understanding the size or significance of these random effects.

We did not explicitly fit intercept terms in the model, since including it in a Bayesian random effects model can sometimes make estimation of the variance components for each random effect difficult. Although data was collected across two different days in two seasons, these factors were not significant contributors to the model and are therefore excluded from the model described here.

Incorporating expert information into the Bayesian model

We now extend the model presented in Eq. 1 to incorporate the prior information from the experts. The expert scores informed us about the means and variances of the random effects, so these were no longer centered on zero with wide intervals. Instead, the prior information was introduced into the model through the construction of another hierarchical layer. More explicitly, the priors in Eq. 1 can be augmented where the random effects are distributed Normally as

$$s_{c_i} \sim N(\mu_{s_c} + \bar{X}_{s_i}, \tau_{s_c}\varepsilon_{s_i}) \qquad c = 0, 1.;$$
$$i = 1, \ldots, 31.,$$
$$g_{c_j} \sim N(\mu_{g_c} + \bar{X}_{g_j}, \tau_{g_c}\varepsilon_{g_j}) \qquad c = 0, 1.;$$
$$j = 1, 2, 3.,$$
$$sg_{c_{ij}} \sim N(\mu_{sg_{ij}} + \bar{X}_{sg_{ij}}, \tau_{sg_c}\varepsilon_{sg_{ij}}) \qquad c = 0, 1.;$$
$$i = 1, \ldots, 31.,$$
$$j = 1, 2, 3., \qquad (2)$$

given Normally distributed means

$$\mu_{s_c}, \mu_{g_c}, \mu_{sg_c} \sim N(0, 0.1) \; c = 0, 1$$

with Gamma priors on the precisions of the variance components

$$\tau_{s_c}, \tau_{g_c}, \tau_{sg_c} \sim Ga(0.1, 0.1) \; c = 0, 1.$$

In contrast to Eq. 1, μ has been introduced into the model for each random effect because the expert has explicitly provided information about variation in the mean. The precision is therefore rescaled (e.g., τ_{s_c}, ε_{s_i}) according to how much in agreement the experts were with regards to changes in the mean. Here, $\bar{X}_{s_i}$, $\bar{X}_{g_j}$, and $\bar{X}_{sg_{ij}}$ represent the expert shift in mean defined for the ith species, the jth grazing level, and the ith species under the jth level of grazing, and ε_{si}, ε_{gj}, and ε_{sgij} represent the rescaling of the precision based on the overall expert response for each factor in the model as shown in Table 2.

In the absence of expert knowledge, we reverted back to the model presented in Eq. 1, which is comprised of non-informative priors for each random effect and their respective parameters. Therefore, the availability of expert opinion allowed us to augment the survey data and establish whether the experts were expressing changes in density that is reflected by the data. If their opinions differed from the survey data, then the Bayesian analysis allows us to quantify and comment on this difference.

Parameter estimation

Parameter estimation was achieved using Markov Chain Monte Carlo (MCMC) and, in particular, the Metropolis Hastings algorithm (Metropolis et al. 1953, Hastings 1970) using WinBUGS 1.4 (Spiegelhalter et al. 2003).

MCMC is an approach that generates a Markov Chain that converges to the posterior distribution of interest using Monte Carlo simulation. For a complete overview of MCMC and related methods, readers are referred to Besag et al. (1995). The algorithm consists of three steps. The first involves setting initial values for unobserved quantities, which represent the variance components and predictions for each random effect in the model. The second involves sampling from each parameter's full conditional distribution, while holding all other parameters constant. Finally, the sampled values for each parameter of interest are monitored for convergence. This is usually achieved after a lengthy burn-in using convergence criterion contained in the CODA package (Best et al. 1995) and described extensively in Cowles and Carlin (1996) and Mengersen et al. (2000). A second run is constructed from which means, standard deviations, and 95% credible intervals can be calculated. Based on these criterion, a burn-in of 10 000 and a further 30 000 iterations were used in this study to get appropriate estimates. This number of iterations gave a suitably low Monte Carlo standard error of the mean (MC error) and level of autocorrelation.

RESULTS

Exploratory analysis of expert data

Survey results from 20 experts were combined to get a mean response to grazing for each species under each level of grazing (Table 2). The precision of responses was smallest under low ($\varepsilon_{\cdot 1} = 2.23$) and moderate ($\varepsilon_{\cdot 2} = 2.22$) levels of grazing compared with high ($\varepsilon_{\cdot 3} = 2.49$) levels. This indicates that the level of agreement amongst the experts was slightly greater under high grazing. Experts predicted an overall increase in mean abundance under low ($\bar{X}_{\cdot 1} = 0.345$) and moderate ($\bar{X}_{\cdot 2} = 0.168$) grazing and a strong decrease under high ($\bar{X}_{\cdot 3} = -0.598$) levels of grazing.

In Table 2, a high precision indicates greater convergence in opinion about a particular species and grazing level. For three species/grazing combinations in particular, all experts were unanimous in their response, leading to a precision of infinity. For these cases, the precision was set to 30, a value larger than any other value in the dataset, yet one that does not dominate the results produced by these precision estimates. Because experts only provided responses for species and grazing levels in which they were confident, the number of response per species varied from 11 to 20.

Pooled expert responses for each species across each grazing level are shown in Fig. 2 for nine species and for the remaining species in Appendix B. A value close to zero indicates experts did not expect a species to respond either negatively or positively to the specified grazing level on average, whereas a high negative value indicates a decline in abundance with the grazing level,

TABLE 2. Information elicited from 20 experts regarding the grazing impact on 31 species of birds in woodland habitats showing the mean response ($\bar{X}_{ij}$) from experts and the corresponding precision (ε_{ij}, the inverse of variance) at different grazing levels.

No.	Species	Code	Grazing impact Low/no (1)		
			n_{i1}	$\bar{X}_{i1}$	ε_{i1}
1	Apostlebird	APOS	14	−0.14	1.69
2	Black-chinned Honeyeater	BCHE	13	0.38	3.90
3	Brown Quail	BRQU	15	0.80	3.18
4	Brown Thornbill	BRTB	18	0.61	3.97
5	Brown Treecreeper	BRTC	19	0.11	1.53
6	Buff-rumped Thornbill	BUTB	17	0.35	1.62
7	Brown-headed Honeyeater	BWHE	14	0.29	4.55
8	White-winged Chough	CHOU	16	0.00	1.88
9	Double-barred Finch	DBFI	14	0.50	1.73
10	Eastern Yellow Robin	EYRO	19	0.63	2.80
11	Fuscous Honeyeater	FUHE	14	0.29	4.55
12	Grey-crowned Babbler	GCBA	19	0.32	2.22
13	Golden Whistler	GOWH	15	0.33	4.20
14	Grey Shrike-thrush	GSTH	17	0.47	2.57
15	Jacky Winter	JAWI	19	0.16	1.71
16	Leaden Flycatcher	LEFC	12	0.25	4.89
17	Noisy Miner	NOMI	18	−0.50	2.00
18	Red-backed Fairy-wren	RBFW	12	0.75	2.59
19	Restless Flycatcher	REFC	15	0.27	2.02
20	Rose Robin	RORO	14	0.64	4.04
21	Rufous Songlark	RUSL	19	0.26	1.54
22	Rufous Whistler	RUWH	17	0.24	5.23
23	Varied Sittella	SITT	15	0.20	5.83
24	Spotted Quail-thrush	SPQT	11	0.09	1.12
25	Speckled Warbler	SPWA	17	0.47	1.94
26	Superb Fairy-wren	SUFW	20	0.65	2.90
27	Variegated Fairy-wren	VAFW	15	0.60	2.50
28	White-naped Honeyeater	WNHE	14	0.36	4.04
29	White-browed Scrubwren	WSCW	18	0.78	5.46
30	White-throated Honeyeater	WTHE	11	0.36	3.93
31	White-throated Treecreeper	WTTC	16	0.19	6.15
$\bar{X}_{\cdot j}$				0.345	
$\varepsilon_{\cdot j}$				2.23	

Note: The notations $\varepsilon_{\cdot j}$ and $\bar{X}_{\cdot j}$ refer to the overall precision (ε) and mean ($\bar{X}$) of all 31 bird species (j) for the grazing level stated in the column heading of Table 2.

and a high positive value indicates an increase in abundance with the grazing level.

Exploratory analysis of field data

An exploratory analysis of the field data revealed that day was not a significant contributor to the model, affecting neither bird presence/absence nor abundance significantly. We therefore pooled across day to investigate the change in species abundance with respect to grazing and season.

Overall, similar numbers of species were recorded over both seasons, with a significant decline in species abundance under high levels of grazing (mean species richness over summer and winter for no/low = 6.1, moderate = 6.5, and high grazing = 3.8). Season was not a significant contributor to the model, and we therefore pooled the data across seasons to eliminate some of the zero values, giving us more power to detect changes in species presence/absence and abundance due to grazing.

Seven species response patterns to grazing emerged from the expert and field data and are defined in Table 3. Fig. 3 contains a graphical representation of the responses for nine species, and the responses for remaining species are shown in Appendix B. Amongst the 31 species examined, the most common responses to grazing observed in the field data were: (1) an absence under high grazing with similar abundances under low and moderate grazing ("High Intolerant" [e.g., White-browed Scrubwren, Superb Fairy-wren]); (2) an "Intermediate" response where density was greatest under moderate grazing (e.g., Fuscous Honeyeater, Red-backed Fairy-wren); or a "Generalist" response where abundance was similar across all grazing levels (e.g., Rufous Whistler, Double-barred Finch). Four species (Brown Thornbill, Rose Robin, Spotted Quail-thrush, and White-naped Honeyeater) only occurred under low levels of grazing ("Low Dependent"). Only one species, the Noisy Miner, increased markedly with increased grazing pressure (Fig. 3). We cannot be con-

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TABLE 2. Extended.

|	Moderate (2)			High (3)	
n_{i2}	$\bar{X}_{i2}$	ε_{i2}	n_{i3}	$\bar{X}_{i3}$	ε_{i3}
14	0.71	4.55	14	0.21	1.05
14	0.00	6.50	13	−0.54	3.71
15	0.20	1.67	15	−1.00	30.00
19	−0.20	3.17	19	−0.79	5.70
19	0.47	1.41	19	−0.68	2.22
18	0.44	2.01	17	−0.71	4.53
16	0.00	7.50	14	−0.43	3.79
17	0.71	2.89	17	−0.18	1.28
14	0.07	1.88	14	−0.93	14.00
19	−0.05	2.01	19	−0.95	19.00
16	0.13	8.57	13	−0.46	3.71
19	0.68	4.38	19	−0.58	2.71
17	−0.18	3.58	16	−0.81	6.15
17	0.29	1.68	17	−0.65	2.72
19	0.74	4.89	19	−0.58	2.09
14	0.07	4.44	13	−0.38	3.90
19	0.42	3.89	19	0.67	2.22
12	−0.33	1.65	13	−1.00	30.00
17	0.29	2.89	16	−0.63	4.00
14	−0.14	2.28	15	−0.80	5.83
19	0.16	1.71	19	−0.42	1.23
19	0.16	3.98	18	−0.61	3.97
17	0.00	8.00	16	−0.38	4.00
12	−0.08	1.59	12	−0.83	6.60
17	0.12	1.16	17	−0.88	4.25
20	0.40	2.16	20	−0.80	5.94
15	0.07	1.08	15	−0.87	8.08
16	0.06	16.00	14	−0.50	3.71
17	−0.47	2.57	18	−1.00	30.00
12	0.08	12.00	12	−0.50	3.67
18	0.00	8.50	18	−0.61	3.97
	0.168			−0.598	
	2.22			2.49	
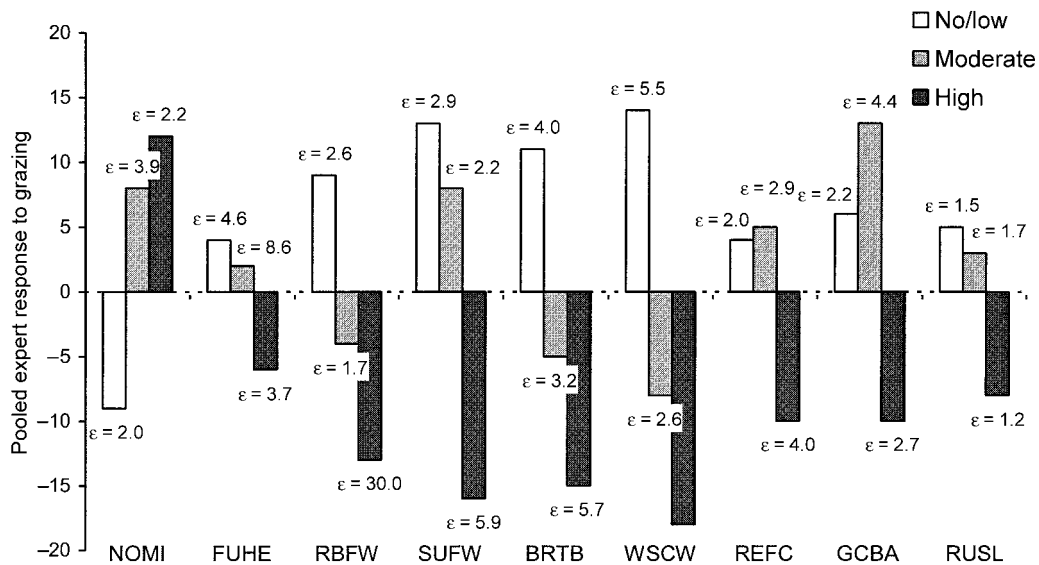
FIG. 2.   Pooled expert opinions on bird response to grazing for nine species. Each bar represents the mean as reported in Table 2, with expert precision (ε) shown at the end of each bar. The line at zero represents the belief that a species will show no response to a particular grazing level, whereas bars above the line indicate an increase in response to the grazing level, and bars below the line indicate a decrease in response to the grazing level. Species codes are defined in Table 2.

TABLE 3. Species response patterns to grazing that emerged from the expert and filed data.

Response to increasing grazing pressure	Abbreviation	Definition
Low Dependent	Low Dep	only occurs in low grazed habitat
High Intolerant >L	High Intol >L	absent under high grazing and highest density under low grazing
High Intolerant >M	High Intol >M	absent under high grazing and highest density under moderate grazing
High Intolerant	High Intol	absent under high grazing and densities similar under low and moderate grazing
Intermediate	Inter	highest density under moderate grazing
Generalist	Gen	similar density across all grazing levels
Increase	Incr	density increasing with increasing grazing pressure

fident of the response of 10 species, denoted with a dagger symbol in Table 4 due to their low frequency ($\leq 6\%$, having occurred at three sites or less in either season; Appendix B).

An exploratory comparison of the expert and field data is shown in Table 4. We did not account for the high frequency of zero values in the field data or the level of precision of the expert data during the exploratory analysis phase of this study. Therefore, results must be interpreted with caution.

In Table 4, the three most common responses predicted by experts were an intolerance of high grazing with highest abundance under no/low grazing levels, an intolerance of high grazing with similar abundances under moderate and high grazing, or a dependence on no/low grazing (absent from moderate and high; Table 4). Overall, 32% (10 species) of expert responses corresponded exactly with the field data (Table 4)

Two-component model predictions

Our interest was in the impact of grazing on individual bird species and this is what we asked the experts to comment on. Results, therefore, focus on the grazing by species random effect.

Predictions from the two-component model are shown in Appendix B, where the predictions from the first component of the model, based on presence/ab-sence data, with and without expert information is presented followed by the predictions from the second component of the model, based on abundance data given presence with and without expert information.

The term ''significance'' is used in the Bayesian context when a significant effect indicates that the 95% credible interval corresponding to that effect does not include zero and an estimate that is ''significantly less than'' a proposed value has <5% probability of being equal to or greater than the proposed value.

Predictions of bird presence/absence: no expert information (non-informative prior)

Only three species (Leaden Flycatcher, White-throated Treecreeper, and Noisy Miner) showed a significant increase in the probability of presence compared to all other species under specific grazing levels, with both the Leaden Flycatcher and White-throated Treecreeper increasing under no/low grazing, and the Noisy Miner increasing under high grazing (Appendix B). Note that predictions for the presence/absence component presented in Appendix B are on the logit scale, where a prediction of zero corresponds to a probability of 0.5.

With expert informative (informative prior)

Combining expert information (prior) with the field data (likelihood) gives us an informed posterior pre- **?1**
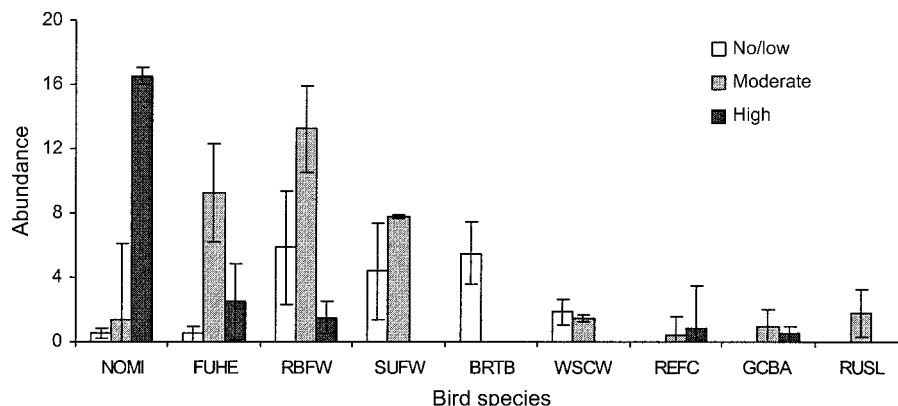

FIG. 3. Abundance (mean ± 1 SE) as observed from the field data for nine bird species across three grazing levels: low/no, moderate, and high. Species codes are defined in Table 2.

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TABLE 4.   Comparison of expert information (prior) with field data (likelihood) across seven response patterns defined in
Table 3.

Expert data	Field data							
	Low Dep	High Intol >L	High Intol >M	High Intol	Inter	Gen	Incr	Total
Low Dep	**BRTB** **RORO†** **SPQT†**			EYRO† WSCW	RBFW	GOWH		7
High Intol >L		**LEFC** **VAFW** **WTHE** **WTTC**		BCHE† BRQU BWHE†	FUHE	DBFI SITT SPWA		11
High Intol >M			...		BRTC‡ GCBA†		REFC	4
High Intol	WNHE†			**BUTB** **SUFW**	JAWI RUSL†‡	GSTH‡ RUWH		6
Inter					...		APOS† CHOU†‡	2
Gen						...		0
Incr							**NOMI‡**	1
Total	4	4	0	7	6	6	4	31

Notes: Boldface indicates where there was complete agreement between the prior and likelihood. Expert data are represented
by the mean response from all experts who responded for a given species. Field data are represented by the mean response
to grazing across both summer and winter. Species with a dagger (†) have a frequency ≤6% (see Appendix B). Species
marked (‡) have a precision <4 under all grazing levels (see Table 2).

diction of each species' probability of presence under
the three grazing levels (Appendix B; Probability of
presence: With expert). In addition to the three species
that had a significant increase in the probability of pres-
ence under no/low and high grazing, respectively, with-
out expert information, a further three species (Brown
Quail, Red-backed Fairy-wren, and White-browed
Scrub-wren) showed a significant decrease in the prob-
ability of presence under high levels of grazing.

Predictions of bird abundance: no expert information (non-informative prior)

Given a species was detected, we modeled abun-
dance using a truncated Poisson distribution. Random

effect predictions for the abundance component of the
two-component model for nine species is shown in Fig.
4, and for the remaining species in Appendix B, with
and without expert information. Predictions are shown
on the log scale. A corresponding scale showing ex-
pected abundance is given on the right hand side of
Fig. 4. Species that showed no change in abundance
are centered on zero (log scale) with confidence inter-
vals spanning −1 and 1. Two species (Fuscous Hon-
eyeater and Noisy Miner; Fig. 4) showed a significant
increase in abundance under moderate and high grazing
levels, respectively. There is a strong trend for species
abundance to be higher under no/low and moderate
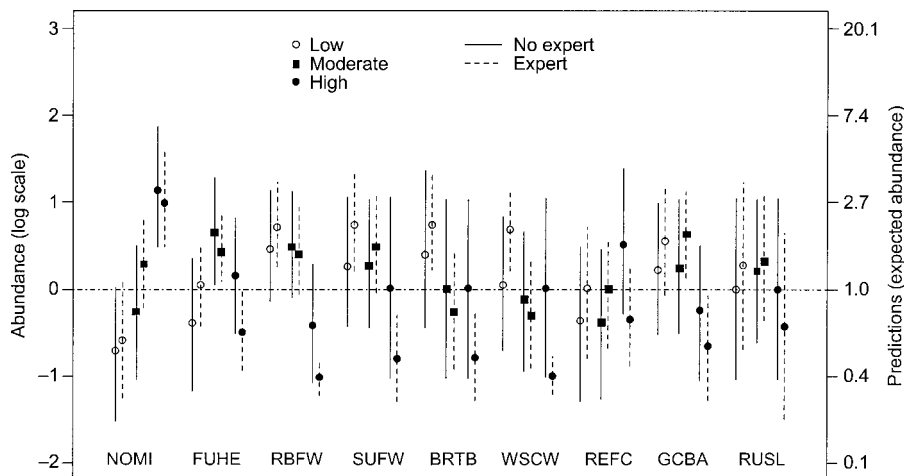levels compared with high grazing, while over half (16

FIG. 4.   Comparison of two-component model estimates of abundance and 95% credible intervals for nine species without
and with expert information for low, moderate, and high grazing levels. Species codes are defined in Table 2.

species) showed strong declines under high grazing levels (see Fig. 4 and Appendix B; Abundance estimate: Without expert).

The addition of the expert data has a notable impact on abundance predictions with increases predicted for all species, with the exception the Apostlebird and Noisy Miner under no/low grazing. Of these increases, eight species increased to a level where the result was significant (see Fig. 4 and Appendix B; Abundance prediction: With expert). Under moderate grazing levels, five species, including the Fuscous Honeyeater and Grey-crowned Babbler, showed a significant increase in abundance, while under high grazing, only one species, the Noisy Miner, showed a significant increase. All other species showed a decrease in abundance under high grazing, 16 of which were significant declines (see Fig. 4 and Appendix B; Abundance estimate: With expert).

DISCUSSION

This paper examines the power of expert opinion to inform ecological models through an investigation of the response of woodland birds to cattle grazing. We have demonstrated how expert knowledge can be collected and used within a Bayesian statistical framework to update our field data to obtain species-specific predictions for the probability of presence and abundance given presence, under varying levels of grazing.

Bayesian inference allows the construction of informative prior probabilities for poorly known effects using auxiliary information obtained from experts, previously published findings, or both (Ghazoul and McAllister 2003). As demonstrated in this paper, the use of expert information moderates field data and strengthens predictions for most species compared to predictions formed in the absence of expert knowledge (Fig. 4, Appendix B).

The simple questionnaire delivered to experts provided a practical tool for eliciting information that was less onerous than other published methods while delivering adequate, repeatable information in a form that was suitable for analysis. Using multiple experts allowed us to generate a mean and precision around the estimates without having to specifically ask each expert for these estimates, a task that would deter many from participating in the survey. We hope that our detailed description of the method by which this prior information was combined with the field data demonstrates the generalizability of the model to other ecological modeling situations.

How much do expert and field data agree with each other in regards to the impact of grazing on birds?

In our exploratory analysis, we found that the responses for 10 species (32%) were in complete agreement with the field data (Tables 3 and 4). Of the remaining species in which the data was strong and the expert precision high, eight species were predicted by

experts to do worse under increasing grazing pressure than what we found in the field. Mismatches occurred primarily where either the field data recorded was poor (low frequency of occurrence) or the expert precision (level of agreement) was low (Table 4).

Does the addition of expert information improve model predictions and under what conditions do they improve?

The addition of the expert information to the model improved predictions considerably, through narrower 95% credible intervals for all but one species under at least one level of grazing (Fig. 4 and Appendix B). The degree of improvement depended on the amount of data, the expert precision under each grazing level, and how well the experts ''pooled'' belief about grazing and its impact on bird presence/absence and abundance agrees with the field data.

In the absence of expert information, when the data was limited or, alternatively, no sightings were made at a particular grazing level, little could be said about whether a species was likely to increase or decrease with respect to grazing. This is particularly evident at high levels of grazing where absences were most common (e.g., White-browed Scrubwren, Eastern Yellow Robin; Fig. 4, Appendix B). When we combined the field data with expert information and the experts agreed and complement the field data, our predictions improved somewhat, providing information about a species' predicted decline or increase that we otherwise would not have known about in the absence of expert information.

Where the data is strong (high frequency of occurrence) and the precision of the expert data is also high, we saw significant improvements in model predictions (e.g., Fuscous Honeyeater and Red-backed Fairy-wren; Fig. 4). Model improvements were also made when the precision and field data were moderate but complement one another (e.g., Superb Fairy-wren, Brown Thornbill, and White-browed scrubwren; Fig. 4).

In situations where the precision of the experts was low, indicating disagreement between experts, the information conveyed by the posterior was no different to what we would have obtained in the absence of expert information. Expert information informs predictions when the experts are in agreement with one another and expresses uncertainty in situations where experts really do not know enough about the subject of interest. For example, the predictions for the Rufous Songlark did not improve with the addition of the expert information. Here, both the precision was low and the amount of field data was weak (low frequency of occurrence; Fig. 4), reflecting the few sightings of this species recorded during the survey and the overall lack of understanding about this species.

Of the species for which we had sufficient field data and the precision was ≥ 4, there were 11 species for which the experts' predictions did not agree with the

field data in our exploratory investigations. For example, the Red-backed Fairy-wren was predicted, by experts, to decrease under moderate and high grazing (Low Dependent), but we observed an intermediate response (Table 4). The Restless Flycatcher was predicted to decrease under high grazing (High Intolerant >M), but we observed an increase with grazing. These two species are explored in more detail in the next paragraphs.

When comparing the raw field data and modeled predictions, we must consider that the conditional model only models abundance if a species is present. It therefore excludes all absences (zero cells). If we examine the Red-backed Fairy-wren as shown in Figs. 3 and 4, its abundance, modeled without expert data, does not reflect the considerable increase observed under moderate grazing as shown in Fig. 3. This is a result of accounting for the inflation of zero values. However, if we look at the results from the first component of the model based on presence/absence (Appendix B), the results do reflect this increased probability of presence under moderate grazing and illustrates the importance of interpreting the two components of the model together.

In the case of the Restless Flycatcher under high grazing, the precision surrounding the expert response is moderate ($\varepsilon = 4.0$; Fig. 4). For this species, the experts were relatively confident that it would do poorly under high grazing, yet the field data suggest otherwise. The prediction of the probability of presence and abundance given presence for this species reflects the experts' confidence in this species' response and is also the result of low numbers reported for this species in the field data (frequency <10%). If there were a larger occurrence of frequency in the field data for this species, the prior based on expert information would not have such a large impact, and it demonstrates that when data is scarce, expert information is a powerful tool in ecological modeling.

The largest improvement in the predictions occurs when the data is weak (low frequency of occurrence) and the precision of the expert information is high. For example, when a species is not observed at a particular grazing level and there is no expert information, the prediction for that species (on the log scale) is zero with wide credible intervals spanning -1 to 1 as illustrated by the White-browed Scrubwren under high grazing (Fig. 4). Given expert information with a high precision, the confidence interval around that prediction narrows, showing a significant decline in abundance under high grazing.

Is expert information useful?

Expert knowledge is a valuable resource to ecology and when combined with field data in a model as illustrated in this study, it has the potential to strengthen results or alternatively highlight areas that require further research, a finding supported by Iglesias and Kothmann (1998).

Certainty about a species and its relationship to a particular disturbance is indicated when experts are in agreement (high precision), whereas uncertainty is expressed when experts are in disagreement (low precision). Alternatively, this uncertainty could reflect a complex species response to disturbance. Responses could vary from one place to another and/or be a reflection of interactions with co-occurring species. Three species (Brown Treecreeper, Rufous Songlark, and White-winged Chough; Fig. 4, Appendix B), in particular, had low precision values, suggesting that further research is needed to require a better understanding of the impacts of grazing on these species.

There are various explanations for a mismatch between the expert opinion and the data. Many factors contribute to an expert's perception of grazing. One could expect that experts with much of their experience in highly developed (relictual and fragmented) landscapes of temperate Australia perceive the impact of grazing differently to those in variegated or intact landscapes of subtropical Australia. For example, in landscapes where tree clearing and grazing are completely confounded it may be difficult for experts to think about these two disturbances independently. Given sufficient information about an expert's background, we could test this by analyzing the data based on where the experts have spent most of their professional lives and have built their beliefs. This subjective judgment, where people interpret and guess differently, is part of what Regan et al. (2002) defines as epistemic uncertainty in ecology and conservation biology.

The fact that experts may carry with them a bias based on their context has been a criticism of using expert information (Dennis 1996). However, given a large independent sample of experts, we believe that this is not an issue. In situations in which experts have different beliefs concerning a particular species and grazing regime, we expect a low precision to be highlighted, which is then propagated through the model.

What does this mean for birds in grazed landscapes?

This study supports the idea that grazed grassy woodlands provide habitat for many species of plants and animals, but some are highly sensitive to the changes brought about by more intense livestock grazing (Martin and Green 2002). Low and moderately grazed grassy woodlands provide habitat for many bird species, but highly grazed areas appear to benefit only one of the 31 species analyzed in this study. The "hyperaggressive" Noisy Miner successfully excludes other woodland species from its territory, eventually dominating large areas of habitat (Piper and Catterall 2003), and therefore the absence of woodland birds in highly grazed areas may be an indirect effect of high grazing by providing ideal habitat for the Noisy Miner.

Moderate levels of grazing in woodland favored several species (e.g., Brown Treecreeper, Grey-crowned Babbler, Jacky Winter, Speckled Warbler) that have been declining in temperate parts of Australia, and this decline has been attributed to vegetation clearing and grazing (Blakers et al. 1984, Garnett and Crowley 2000). In temperate Australia, these disturbances are often confounded (e.g., Arnold and Weeldenburg 1998, Jansen and Robertson 2001). It appears that in the landscapes studied here, where we can separate the effect of grazing from tree clearing, these birds respond positively to moderate levels of grazing. Here, livestock grazing may be replacing the natural disturbances caused by fire and macropod grazing in which these species specialized. The majority of experts predicted this response.

Species associated with no/low levels of grazing in this study (Brown Thornbill, Leaden Flycatcher, Variegated Fairy-wren, White-throated Honeyeater, White-throated Treecreeper) have been characterized in the Southeast Queensland Bioregion by Catterall et al. (1998) as ''bushland'' species, occurring in forest/woodland with an understorey of shrubs and/or grasses. The increased cover of shrubs, large tussock grasses, and lack of general disturbance by cattle in our no/low grazing treatment provides ideal habitat for these species. Furthermore, saplings provide a mid-story, whereas, even in moderately grazed sites, sapling recruitment can be inhibited by grazing (Martin et al. 2000).

Conclusion

Financial and logistical constraints impair our ability to sample over large geographic areas and long time frames resulting in few long-term ecological data sets. In situations such as this, expert knowledge can be used to capture information beyond the study region and is the culmination of many years experience.

Using expert data in combination with our field study enabled us to gain a greater insight into the overall impacts of livestock grazing on birds than we would have in the absence of expert information. In fields where there is extensive expert knowledge, yet little published data (e.g., rare species), the use of expert information as priors for ecological models is a cost-effective way of making more confident predictions about the effect of management on biodiversity.

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APPENDIX A

An example of an expert survey is available in ESA's Electronic Data Archive: *Ecological Archives* XXX.

APPENDIX B

A summary of field and expert data and results from a two-component model with and without expert information is available in ESA's Electronic Data Archive: *Ecological Archives* XXX.