

Assessing the impacts of grazing levels on bird density in woodland habitat: a Bayesian approach using expert opinion

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SUMMARY

Many studies on birds focus on the collection of data through an experimental design, suitable for investigation in a classical analysis of variance (ANOVA) framework. Although many findings are confirmed by one or more experts, expert information is rarely used in conjunction with the survey data to enhance the explanatory and predictive power of the model.

We explore this neglected aspect of ecological modelling through a study on Australian woodland birds, focusing on the potential impact of different intensities of commercial cattle grazing on bird density in woodland habitat.

We examine a number of Bayesian hierarchical random effects models, which cater for overdispersion and a high frequency of zeros in the data using WinBUGS and explore the variation between and within different grazing regimes and species. The impact and value of expert information is investigated through the inclusion of priors that reflect the experience of 20 experts in the field of bird responses to disturbance.

Results indicate that expert information moderates the survey data, especially in situations where there are little or no data. When experts agreed, credible intervals for predictions were tightened considerably. When experts failed to agree, results were similar to those evaluated in the absence of expert information. Overall, we found that without expert opinion our knowledge was quite weak. The fact that the survey data is quite consistent, in general, with expert opinion shows that we do know something about birds and grazing and we could learn a lot faster if we used this approach more in ecology, where data are scarce. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: Australian woodland birds; Bayesian modelling; elicitation; impact of grazing; Markov chain Monte Carlo; mixtures; random effects; WinBUGS; zero-inflated count data

1. INTRODUCTION

The hypothesis that bird numbers for woodland species decline under high levels of commercial cattle grazing—a land use that is extensive across most continents—has obvious implications for the

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conservation of Australian birds in rural landscapes. Several studies have attempted to assess the impact of grazing on birds using standard classical methods such as analysis of variance (ANOVA) but they have been hindered by the confounding of grazing with other disturbances such as tree clearing (Arnold and Weeldenburg, 1998; Jansen and Robertson, 2001) and limited data (Sedgwick and Knopf, 1987; Popotnik and Guiliano, 2000; Soderstrom *et al.*, 2001; James, 2003).

Remarkably, findings from analyses like these, whether statistically significant or not, are often confirmed by one or more experts in the field. It therefore seems appropriate to incorporate this expert knowledge into an analysis to moderate the results obtained from surveys. However pragmatic this seems in ecology, this idea has not been widely promoted (Carpenter, 2002). Inexperience concerning how to introduce expert information into the model as a prior and how the results from the model can be interpreted, prohibit its use. There is also a great deal of skepticism about the role of a prior (elicited from an expert) in a model and the concern that a prior of this type may drive the modelling process rather than guide it (Dennis, 1996). In this article, we explore the role that expert information might play as an integral part of modelling and analysis rather than a mere validation check after analysis.

A second purpose of this article is to explore the Bayesian framework using two types of models for count data. In situations like these, zeros can be ambiguous, that is, either the birds are present but not detected (random) or else they are absent altogether (structural). We use a random effects model for zero-inflated (ZI) count data, developed in a Bayesian framework (with and without expert information) to examine the impact of grazing on bird numbers. We investigate two types of models to cater for the excess number of zeros. The first is a conditional approach, sometimes referred to as a two-component approach that models the presence or absence of a species using logistic regression and then, conditional on presence, abundance is modelled through a truncated discrete distribution such as the truncated negative Binomial or truncated Poisson. This orthogonal parameterization has an intuitive appeal because it allows the investigator to interpret the impacts of grazing on the presence or absence of a species separately from its impact on abundance.

A slightly more complicated model, but one that allows the specification of structural and random zeros in the data is a mixture model comprised of a mixture of a point mass at zero and a Poisson distribution (Lambert, 1992). The interpretation of this model becomes somewhat complicated because the parameterization is not orthogonal, therefore requiring the investigator to interpret impacts on abundance in conjunction with whether a zero is treated as structural or random.

Models for zero-inflated count data have been discussed rigorously by Lambert (1992), Heilbron (1994), Welsh *et al.* (1996, 2000) and Dobbie (2001), among others. These models have been applied to numerous problems including the assessment of the number of defects in a manufacturing process (Lambert, 1992), the estimation of the number of Leadbeater possums in the forests of south-eastern Australia (Welsh *et al.*, 1996; Faddy, 1998; Podlich *et al.*, in press), prevention in dental epidemiology (Bohning *et al.*, 1999), evaluation of an occupational injury prevention program (Yau and Lee, 2001) and investigation of manual handling injuries and their relationship with exposure (Lee *et al.*, 2001). Extensions to zero-inflated count methods include the work of Dobbie and Welsh (2001a) and Dobbie and Welsh (2001b), who investigated methods of correlated zero-inflated count data; the work of Agarwal *et al.* (2002), who developed Bayesian methods for spatial count data exhibiting excess zeros; and Barry and Welsh (2002), who investigated a flexible method for modelling zero-inflated count data using generalized additive models.

There has been considerable discussion concerning elicitation methods in the statistics literature and how they can be used to create a prior and inform an analysis (Garthwaite and Dickey, 1988, 1992, 1996; Steffey, 1992; O'Hagan, 1998; Landrum and Normand, 1999; Garthwaite and O'Hagan, 2000).

As identified by these and other researchers, there is a fine art to elicitation, one that involves extracting probabilistic statements from one or more experts in an easy framework without subjecting the expert or experts to complex mathematical formulae or difficult terminology. Typically, elicitation is performed using one expert, although the process may involve several experts, depending on the problem at hand.

When one expert is used, the elicitor needs to be aware of a number of pitfalls as summarized by Kadane and Wolfson (1998). In particular they cite: *hindsight bias*, where elicited priors have already been updated by data; *availability*, where experts provide a frequency of an event rather than a probability; *overconfidence*, where an expert does not assess the tails of the distribution adequately; and *adjustment and anchoring*, where the expert's opinion is anchored incorrectly, as the main traps to avoid when eliciting information from a single expert. Kadane and Wolfson (1998) also promote asking predictive rather than structural questions, with a focus on asking questions about observable quantities, where the expert provides a mean and quantiles corresponding to the predictive distribution of the quantity of interest.

Elicitation using multiple experts where the information is obtained separately and then combined in some way is known as the Delphi method and it has been discussed by a number of authors (French, 1985; Genest and Zidek, 1986; Chatterjee and Chatterjee, 1987; Jacobs, 1995). Those who expressed reservations about this approach include McConway (1981), Schervish (1986), O'Hagan (1998) and Roback (2001). O'Hagan (1998), in particular, states his reservations on combining probabilities elicited from experts and promotes the group consensus approach to eliciting information from multiple experts. Furthermore, he promotes preliminary training of experts as an integral part of the elicitation process. Although this represents an 'ideal' situation for eliciting information from a group of experts, realistically, this cannot often be achieved, especially when the experts are geographically disparate and time and monetary constraints prohibit bringing the experts together in one geographic location. These methods can also suffer from domination by one expert, thus making it more difficult to obtain true information about the variability between experts' opinions, which is a necessary parameter in the analysis of this article.

In ecology, elicitation of expert information, whether obtained from a single expert or multiple experts and the incorporation of these priors into a model, is relatively new and has been highlighted as having an important role in ecological applications, particularly in communicating uncertainty in forest research (Ghazoul and McAllister, 2003). Past research has focused on the comparison of expert information with survey data rather than explicit incorporation of expert information into a model (Lawrence *et al.*, 1997), and the examination of expert information (elicited from several experts), in particular, their level of agreement in response to a particular ecological parameter and summary statistics describing trends across different management scenarios (Alho *et al.*, 1996; Iglesias and Kothmann, 1998). Iglesias and Kothmann (1998), in particular, conducted a study with a similar purpose to ours, focusing on the impact of cattle grazing and fire on plant species. In this study the authors examined the experts' responses using standard agreement statistics and did not directly incorporate expert information in a Bayesian framework. Only one author that we know of has attempted to explicitly incorporate expert information into a model for an ecological problem (Crome *et al.*, 1996). Approaches have remained focused on summarizing expert information and using this in a simulation based model to explore the results (Musacchio and Coulson, 2001; Yamada *et al.*, 2003) or alternatively using experts at different stages of the modelling process to inform analyses (Pearce *et al.*, 2001).

The study presented in this article involves a small scale survey of Australian woodland birds, where expert information was obtained from 20 ecologists who are considered experts in the field of

bird response to disturbance. These experts are located in various regions across Australia, therefore making group elicitation difficult. Details of the survey design and the process of elicitation are further described by Martin *et al.* (2005). Whereas the focus of that article is on the ecological interpretation and implications of one particular model, this article focuses more specifically on the statistical methods and modelling approaches: choices, consequences and interpretations.

We extend upon the approaches presented by Iglesias and Kothmann (1998) and attempt to pool information gathered from experts to investigate how expert information compares with, and supports or refutes, survey data collected on birds and their response to grazing. We chose to use a general scoring system rather than asking an expert to provide a probabilistic statement or statements about a bird's expected count at different quantiles of some probability distribution, a technique promoted by Kadane and Wolfson (1998) and Garthwaite and Dickey (1988, 1992, 1996). Furthermore, we chose not to ask the experts about their uncertainty in the form of a variance or standard deviation, as it was unlikely that we would obtain accurate and informative measures, let alone replicate the exercise, simply because ecologists find measures such as these difficult to quantify. The aim here is to evaluate a much more simple method that elicits estimates of relative change, and use the multiple experts to quantify the degree of precision in these estimates. We summarize the data elicited from experts and incorporate this into a random effects model that is specifically designed to cater for excess zeros in the data as well as any overdispersion.

We begin with an overview of the methods for collecting the survey data and describe the methods used for eliciting information from 20 experts in Section 2. Models for zero inflated count data constructed in a Bayesian framework with and without expert information are discussed in Section 3. The random effect predictions are presented in Section 4, followed by a comprehensive comparison of models and assessment of convergence to determine the best fit. Finally, in Section 5, we present a discussion of the approach.

2. SURVEY METHODS

2.1. Survey design and study region

Woodland habitats, located in the South-East Queensland Bioregion in Australia (Sattler and Williams, 1999), were surveyed to determine the potential impact of commercial cattle grazing on bird numbers across 24 sites, replicated on two separate days and over two seasons. The study region is bounded by 26–28°S and 151–153°E and covers an elevation range of 300–550 m.

Survey sites were stratified across land types over an area of 1000 km² with sites a minimum of 1 km apart. Sites were chosen based on the floristic and structural effects of grazing measured using a combination of aerial photos, topography and soil maps, followed by ground truthing. Knowledge of plant species composition (McIntyre *et al.*, 2002; McIntyre and Martin, 2002; McIntyre *et al.*, 2003) 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 the treatment, representing three levels of grazing: low/no grazing, moderate grazing and high grazing (Martin *et al.*, 2005).

Each of the 24 survey sites consists of a 2 ha search area, where counts of bird species were recorded over 20 min on two separate days and repeated for each season (summer and winter). All birds flying 20 m above the site were excluded, with the exception to aerial feeders, consisting of swifts, swallows and raptors. A complete list of species and their scientific names ordered by family is provided in Appendix 2 of Martin *et al.* (2005). (Note that the ordering shown in this table reflects species identifications 1–31 used in this article.)

A single observer, the second author, completed all surveys to avoid inter-observer variability. Bird counts were made on fine mornings in summer (November–January 2001–2002) between 0445 and 0945 and in winter (June–July 2002) between 0645 and 1145. During summer, surveys were not conducted when the temperature rose above 35°C or during winter when the temperature dropped below –2°C.

To avoid sampling bias, a restricted random visitation method was used (MacNally and Horricks, 2002). This involved partitioning the entire survey region into six geographical groups, visiting each group and the sites within each group, randomly. Like the study by MacNally and Horricks (2002), the restricted approach is necessary because of the difficulties associated with surveying a large region.

2.2. Eliciting priors from the expert

Thirty-two experts with extensive experience in bird responses to disturbance and field experience in grazed landscapes were asked to rank how they thought 31 woodland bird species would respond to cattle grazing. Experts were asked to provide a simple rating: positive (+1), negative (–1) or zero (0) value depending on whether they thought a species was likely to increase, decrease or show no change under low, moderate and high levels of grazing. Only 20 experts completed the survey, providing information for 31 species of woodland birds.

Table 1 summarizes the information elicited from the 20 experts. In Table 1, n_{ij} represents the number of experts who reported on the i th species for the j th grazing regime; \bar{x}_{ij} and τ_{ij} represent, respectively, a summary (the mean and precision or inverse variance) of the experts' belief about how grazing regime j impacts species i ; quantities $\bar{x}_{.j}$ and $\tau_{.j}$ represent, respectively, the mean and precision of the experts' belief about how grazing regime j affects bird species on average in the population; and \bar{x}_i and τ_i represents the mean and precision of the expert's opinion regarding abundance of each species irrespective of grazing. Note that in some instances an expert did not provide information about a species. This occurred when the expert was either unfamiliar with the species or unfamiliar with the species in a particular level of grazing. Hence n_{ij} is not always equal to 20 in the computation of the means and precisions reported in Table 1.

In situations where all experts were in agreement with one another, the estimate of the precision was infinity. Because we wish to allow for the fact that such unanimous agreement might not be evident among a larger cohort of experts, and also to avoid domination of results by these point estimates, in these cases the precision of a species was set to 30 (which corresponds to a variance of 1/30), a value that is larger than any other value in the dataset and a result that is reflective of what we envisage in practice. High precision values were calculated for species 1, 6 and 7, where all experts reported a decline (–1) in the species under high levels of grazing.

3. STATISTICAL ANALYSIS

Modelling the number of birds y_{ijk} , for the i th species at the j th grazing level and the k th site, is undertaken in a generalized linear modelling framework using a Poisson distribution, as is usual for count data. Random effects investigated were included to express the variability between species, grazing regimes and between species within a specific grazing regime.

There is an expectation, however, with the data collected, that the data will exhibit a large number of zeros (see the exploratory data analysis in Section 4.1). It is important to consider methods which cater for data of this type, otherwise the results from the model could be severely biased and lead to

Table 1. Information elicited from 20 experts about the relative impact that three levels of grazing has on bird abundance in woodland habitat. Means (\bar{x}), corresponding precisions (τ) and the number of expert responses (n) are reported for each species, grazing level and species within grazing level. Appendix 2 of Martin *et al.* (in press) contains a complete listing of all 31 species

Species	Grazing impact										
	None/Low (1)			Moderate (2)			High (3)			\bar{x}_i	(τ_i)
	n_{i1}	\bar{x}_{i1}	(τ_{i1})	n_{i2}	\bar{x}_{i2}	(τ_{i2})	n_{i3}	\bar{x}_{i3}	(τ_{i3})		
1	15	0.800	(3.18)	15	0.200	(1.67)	15	-1.000	(30.00)	0.000	(1.16)
2	16	0.188	(6.15)	18	0.000	(8.50)	18	-0.611	(3.97)	-0.154	(3.45)
3	19	0.105	(1.53)	19	0.474	(1.41)	19	-0.684	(2.22)	-0.035	(1.22)
4	20	0.650	(2.90)	20	0.400	(2.16)	20	-0.800	(5.94)	0.083	(1.39)
5	15	0.600	(2.50)	15	0.067	(1.08)	15	-0.867	(8.08)	-0.067	(1.20)
6	12	0.750	(2.59)	12	-0.333	(1.65)	13	-1.000	(30.00)	-0.216	(1.19)
7	18	0.778	(5.46)	17	-0.471	(2.57)	18	-1.000	(30.00)	-0.226	(1.32)
8	17	0.471	(1.94)	17	0.118	(1.16)	17	-0.882	(4.25)	-0.098	(1.18)
9	18	0.611	(3.97)	19	-0.263	(3.17)	19	-0.789	(5.70)	-0.161	(1.74)
10	17	0.353	(1.62)	18	0.444	(2.01)	17	-0.706	(4.53)	0.038	(1.42)
11	18	-0.500	(2.00)	19	0.421	(3.89)	19	0.684	(2.22)	0.214	(1.55)
12	14	0.286	(4.55)	16	0.125	(8.57)	13	-0.462	(3.71)	0.000	(3.50)
13	13	0.385	(3.90)	14	0.000	(6.50)	13	-0.538	(3.71)	-0.050	(2.81)
14	11	0.364	(3.93)	12	0.083	(12.00)	12	-0.500	(3.67)	-0.029	(3.10)
15	14	0.357	(4.04)	16	0.063	(16.00)	14	-0.500	(3.71)	-0.023	(3.31)
16	14	0.286	(4.55)	16	0.000	(7.50)	14	-0.429	(3.79)	-0.045	(3.61)
17	19	0.158	(1.71)	19	0.737	(4.89)	19	-0.579	(2.09)	0.105	(1.42)
18	14	0.643	(4.04)	14	-0.143	(2.28)	15	-0.800	(5.83)	-0.116	(1.59)
19	19	0.632	(2.81)	19	-0.053	(2.01)	19	-0.947	(19.00)	-0.123	(1.40)
20	19	0.316	(2.22)	19	0.684	(4.39)	19	-0.579	(2.71)	0.140	(1.61)
21	15	0.200	(5.83)	17	0.000	(8.00)	16	-0.375	(4.00)	-0.062	(4.35)
22	11	0.091	(1.12)	12	-0.083	(1.59)	12	-0.833	(6.60)	-0.286	(1.47)
23	15	0.333	(4.20)	17	-0.176	(3.58)	16	-0.812	(6.15)	-0.229	(2.30)
24	17	0.235	(5.23)	19	0.158	(3.98)	18	-0.611	(3.97)	-0.074	(2.69)
25	17	0.471	(2.57)	17	0.294	(1.68)	17	-0.647	(2.72)	0.039	(1.47)
26	12	0.250	(4.89)	14	0.071	(4.44)	13	-0.385	(3.90)	-0.026	(3.46)
27	15	0.267	(2.02)	17	0.294	(2.89)	16	-0.625	(4.00)	-0.021	(1.88)
28	16	0.000	(1.88)	17	0.706	(2.89)	17	-0.176	(1.28)	0.180	(1.47)
29	14	-0.143	(1.69)	14	0.714	(4.55)	14	0.214	(1.05)	0.262	(1.46)
30	14	0.500	(1.73)	14	0.071	(1.88)	14	-0.929	(14.00)	-0.119	(1.35)
31	19	0.263	(1.54)	19	0.158	(1.71)	19	-0.421	(1.23)	0.000	(1.33)
\bar{x}_j		0.345			0.168			-0.598			
τ_j		(2.23)			(2.22)			(2.49)			

inferences that are not reflective of the data collected. Furthermore, simple transformations such as square root and log transformations to make the data appropriate for modelling using standard statistical distributions such as Poisson or normal are inappropriate for this type of data because they do not deal with the zeros efficiently. Usually there are so many zeros that transformations do not have the desired effect of symmetrizing the data and eliminating dependence between the mean and variance. This impels a focus on methods for explicitly catering for the excess zeros in a model and understanding why so many zeros have been observed throughout the study.

A zero in the dataset can be caused by one of four different sources of error. The first is structural error, where a bird does not visit a site because it does not represent a suitable habitat. The second is design error, which represents a source of error that occurs due to the structure of the sampling and survey design, that is, the bird is not observed because of how the survey design is set up. The third is observer error, the most common source of error in ecological studies, which corresponds to the error incurred when an observer misses a bird, despite it actually being there. The fourth source of error is what we refer to as 'bird' error. This arises when the bird, despite there being a suitable habitat, chooses not to visit the site or alternatively it is the result of an inadequate understanding of the species habitat requirements and therefore leads to a misspecification of the habitat in the model. In this particular study, we have all four sources of error acting and they can be accommodated easily in zero-inflated models such as the mixture model and the two-component model described in Section 1 and explained in detail in Section 3.

Given that we can model zero inflated count data using mixture and two-component models, it is important to understand how each model accommodates the overinflation of zeros. Figure 1 shows how each model treats the high frequency of zeros in the data. Although in this diagram false positives are displayed, we do not acknowledge false positives, that is, the error due to identifying a species wrongly as a source of error in this study because we believe that it is not an issue. In the two-component model (Figure 1a), observed absences, irrespective of whether truly absent, are modelled separately to the observed presences. Therefore, the structural zeros and the random zeros defined as false negative errors due to the survey design, the behaviour of the bird and the experience of the observer are modelled together. They are modelled in this way to provide an orthogonal parameterization and hence produce a model with parameters that are easy to interpret. In the mixture model shown in Figure 1(b), however, the structural zeros are separated out from the random zeros. This specification allows you to examine the different sources of error acting in the study. However, the parameters in the model become more difficult to interpret since absence is modelled as either a structural zero or a random zero.

We choose to model in a Bayesian framework so that expert information can be easily accommodated in the model. The choice of whether to treat certain factors in the model as fixed or random was based on information gathered from the experts. As described in Section 2.2, the experts were asked to comment on whether, under a particular grazing regime, birds would be likely to increase, decrease or remain unchanged in the general population. Since their responses focused on a shift in mean abundance (downward, upward or showing no change), the focus is on the variability in abundance that could be attributed to a particular grazing regime rather than the impact of fixed effects

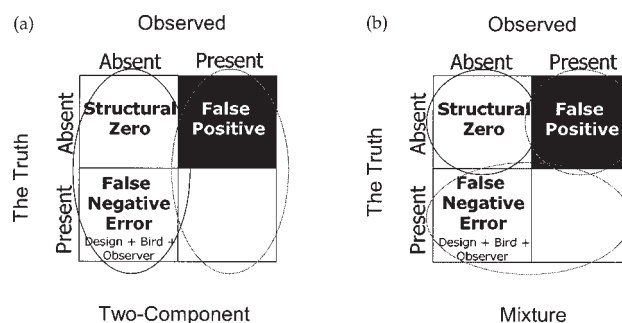


Figure 1. Diagrams showing how the zeros are modelled in the (a) two-component model and (b) mixture model

on the mean abundance. Therefore it seemed reasonable to model each component of the model as random effects.

We investigate two different types of approaches for modelling this data in the following sections. All models were fitted using the free software WinBUGS (Spiegelhalter *et al.*, 2003).

3.1. Two-component model

Equation (1) represents the conditional random effects model for modelling the counts y_{ijk} for the i th species under the j th grazing regime for the k th site. The first component models the probability of presence based on these random effects, while the second component models abundance, conditional on presence based on different random effects. In (1), s_{0i} and s_{1i} represent the species random effects for the presence or absence of the species and abundance, respectively; g_{0j} and g_{1j} represent the grazing random effects for the j th grazing level; and the component that examines the variability of species within the grazing regime is expressed by gs_{0ij} and gs_{1ij} for each model, respectively. We have excluded fitting an explicit mean since its inclusion can sometimes be difficult. In WinBUGS, the mean can be teased out of the first random effect without explicitly specifying a prior for it.

Priors for the random effects consisted of non-informative Normal priors with a mean of zero and precision parameters $\tau_{g_c}, \tau_{s_c}, \tau_{gs_c}$ ($c = 0, 1$). The priors for the precision parameters were chosen to be gamma distributed. We found problems with setting vague priors for the precision parameters as they often proposed values that were unrealistic and distorted the results for the study under investigation.

The model shown in (1) is written as two separate models, reflecting the two components that we wish to model. The first component models the presence or absence of species of birds using logistic regression, while the second models the abundance of birds given presence through a truncated Poisson distribution. A useful feature of this parameterization model is that it simplifies the interpretation of model parameters by estimating random effect variance components for the presence or absence of a species and then, conditional on a species being present, abundance can be modelled through the random effects. Furthermore, each model does not have to contain the same random effects, allowing different variance components to be estimated for each random effect in the model.

The model for presence/absence is

$$z_{ijk} \sim \text{Bernoulli}(p_{ijk}) \quad k = 1, \dots, 8$$

where

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

and with a logit link to random effects

$$\text{logit}(p_{ijk}) = s_{0i} + g_{0j} + gs_{0ij}.$$

The model for abundance conditional on presence is

$$y_{ijk} \mid z_{ijk} = 1 \sim \text{truncated Poisson}(\lambda_{ijk})$$

with a log link to random effects

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

Random effects are distributed normally as

$$\begin{aligned} s_{ci} &\sim \mathbf{N}(0, \tau_{sc}) & c = 0, 1; i = 1, \dots, 31 \\ g_{cj} &\sim \mathbf{N}(0, \tau_{gc}) & c = 0, 1; j = 1, 2, 3 \\ sg_{cij} &\sim \mathbf{N}(0, \tau_{sgc}) & c = 0, 1; i = 1, \dots, 31; j = 1, 2, 3 \end{aligned}$$

with gamma priors on the precisions of the variance components

$$\tau_{sc}, \tau_{gc}, \tau_{sgc} \sim \text{Ga}(0.1, 0.1) \quad c = 0, 1. \quad (1)$$

3.2. Mixture model

The mixture model is specified differently compared to the two-component model. It takes the approach that counts arise from a mixture of a point mass at zero and a Poisson distribution with an unknown probability assigned to each component and unknown parameters for each component. The parameterization for this particular model is not orthogonal, therefore making the interpretation of parameters in the model complicated by the fact that zeros are either treated as structural or random.

In (2), p_{ijk} represents the mixture probability, that is, the probability that a zero is modelled as a Poisson distribution or alternatively, as a random zero. The parameter in the Poisson distribution, λ_{ijk} represents the expected number of birds sighted given that the zeros are modelled in this way. Here, the link function and therefore the random effects for p_{ijk} are interpreted as influencing balance between absence and presence processes rather than focusing on zero abundance (which can arise from both absences and presences) versus non-zero abundance, as specified and modelled in the two-component model.

Priors for each random effect and for the precision parameters were chosen to be non-informative with specifications similar to what was described for the two-component model.

The mixture model is specified as

$$p(y_{ijk} | p_{ijk}, \lambda_{ijk}) = 1 - p_{ijk} + p_{ijk}f(y_{ijk} | \lambda_{ijk}), \quad k = 1, 2, \dots, 8$$

where

$$f(y_{ijk} | \lambda_{ijk}) \sim \text{Poisson}(\lambda_{ijk})$$

and with a logit link to random effects

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

and a corresponding log link to random effects

$$\log(\lambda_{ijk}) = s_{1i} + g_{1j} + sg_{1ij} \quad (2)$$

given normally distributed random effects

$$\begin{aligned} s_{ci} &\sim \mathbf{N}(0, \tau_{s_c}) & c = 0, 1; i = 1, \dots, 31 \\ g_{cj} &\sim \mathbf{N}(0, \tau_{g_c}) & c = 0, 1; j = 1, 2, 3 \\ sg_{cij} &\sim \mathbf{N}(0, \tau_{sg_c}) & c = 0, 1; i = 1, \dots, 31; j = 1, 2, 3 \end{aligned}$$

and gamma priors on the precisions of the variance components

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

3.3. Overdispersion

Overdispersion can be investigated in (1) and (2) by replacing the truncated Poisson and Poisson distributions with a truncated negative binomial and negative binomial distribution, respectively. The negative binomial distribution, as highlighted by McCullagh and Nelder (1989a) and Lawless (1987) deals with extra-Poisson variation (i.e. variation beyond what the Poisson distribution can explain) in a regression model through an explicit dispersion parameter, δ . When this parameter is estimated to be zero, we revert back to the models presented in (1) and (2). Other methods for dealing with overdispersion are considered by Besag *et al.* (1995), among others.

3.4. Estimation

Estimation of the variance components and random effects in each model is 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). The ‘zeros trick’ rule allowed the specification of the truncated Poisson and truncated negative binomial sampling distributions and was also useful for specifying the mixture components of the model presented in (2). Convergence assessment of the Markov chains was examined using the CODA package (Best *et al.*, 1995) using diagnostics described extensively in Besag *et al.* (1995), Cowles and Carlin (1996) and Mengersen *et al.* (2000). We achieved convergence after 10 000 iterations and obtained summary measures such as means, standard deviations and 95 per cent credible intervals using a further 30 000 iterations. The WinBUGS code, together with a copy of the dataset, is available on request by emailing the authors.

3.5. Incorporating expert information into the Bayesian model

Equations (1) and (2) may be extended to incorporate prior information through the construction of an additional hierarchical layer in each zero-inflated (ZI) model as shown in (3).

The model for zero-inflated (ZI) count data is

$$y_{ijk} \sim \text{ZI}(p_{ijk}, \lambda_{ijk}) \quad k = 1, \dots, 8$$

with a logit link to random effects

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

and a corresponding log link to random effects

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

given normally distributed random effects

$$\begin{aligned} s_{ci} &\sim N(\mu_{s_c} + \bar{x}_{s_i}, \tau_{s_c} \epsilon_{s_i}) & c = 0, 1.; i = 1, \dots, 31 \\ g_{cj} &\sim N(\mu_{g_c} + \bar{x}_{g_j}, \tau_{g_c} \epsilon_{g_j}) & c = 0, 1.; j = 1, 2, 3 \\ sg_{cij} &\sim N(\mu_{sg_c} + \bar{x}_{sg_{ij}}, \tau_{sg_c} \epsilon_{sg_{ik}}) & c = 0, 1.; i = 1, \dots, 31.; j = 1, 2, 3 \end{aligned}$$

given normally distributed means

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

and gamma priors on the precisions of the variance components

$$\tau_{s_c}, \tau_{g_c}, \tau_{sg_c} \sim \text{Ga}(0.1, 0.1) \quad c = 0, 1. \tag{3}$$

In (3), \bar{x}_{s_i} , \bar{x}_{g_j} and $\bar{x}_{sg_{ik}}$ represent, respectively, the ‘expert’ shift in mean defined for the i th species, the j th level of grazing and the i th species under the j th level of grazing and ϵ_{s_i} , ϵ_{g_j} and $\epsilon_{sg_{ij}}$ represent the corresponding precision of the experts’ opinions. The distribution ZI represents the zero inflated model (either two-component or mixture model) chosen for modelling the data. Non-informative but proper priors with precisions that reflect what we would expect to observe in the study region were chosen for all other terms in the model.

Although the experts were asked to comment on the impact of grazing on birds explicitly, we were also able to ascertain the pooled expert opinion regarding the overall abundance of each species irrespective of grazing and the overall impact of grazing irrespective of species. Note that, in the absence of expert knowledge, we revert back to the models presented in (1) and (2), which are comprised of non-informative but proper priors for each random effect and their respective hyperparameters.

4. RESULTS

Bayesian analysis allows many probability statements to be made about the model parameters and predictions. In this section we focus on point and interval estimates of the posterior random effects and the overdispersion parameter. Unless stated otherwise, credible intervals comprise density regions excluding 2.5 per cent from each tail of the simulated distributions. Statements of ‘significance’ are made in the Bayesian context, so that a ‘significant’ effect indicates that the 95 per cent credible interval corresponding to that effect does not include zero, and an estimate that is ‘significantly less than’ a proposed value, K say, has less than 5 per cent probability of being equal to or greater than K . The term ‘estimates’ of the random effect reflect estimates of the variance, while ‘predictions’ refer to predictions of the random effect, that is, predicted values on the realizations of the random variable.

4.1. Exploratory data analysis

We performed an exploratory analysis of the data prior to embarking on the statistical modelling to examine the structure of the data. Figure 2(a) shows a plot of the raw data depicting counts for 31

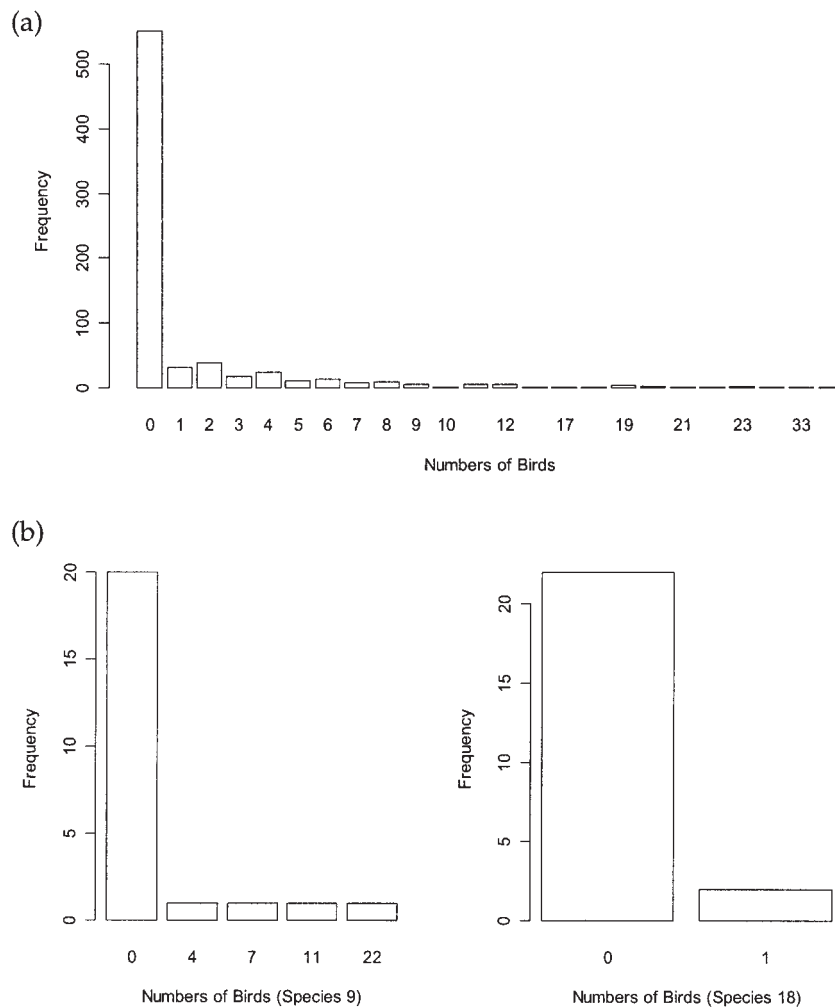


Figure 2. Barplot showing the frequency of bird counts recorded in (a) the entire survey and (b) for two representative species (9,18)

species of birds across eight sites and three treatments ($n = 744$). We pooled across season and day as these factors did not show significant differences between bird numbers in our preliminary investigations of the data. Figure 2(b) shows plots of the raw data ($n = 24$) for two representative birds in the dataset, species 4 and 20.

An obvious feature of the plots shown in Figure 2 is the large number of zeros present in the data. This was highlighted in Section 3 as a feature of the dataset that warranted further investigation. In fact, over 70 per cent of the entire dataset is represented by zero counts, which is more than expected if a Poisson distribution is assumed for bird abundance. There is also some suggestion of overdispersion in the data due to the high nature of some of these counts, although this is difficult to confirm without properly accounting for the excess number of zeros.

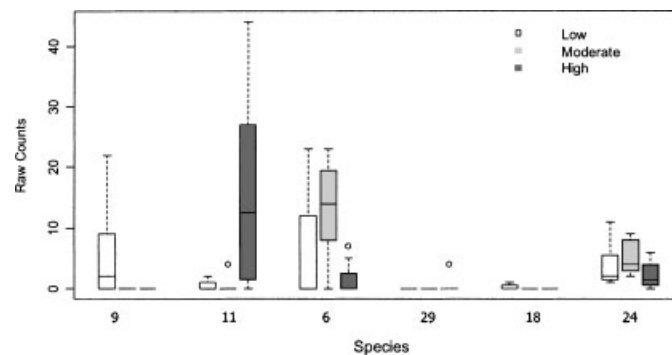


Figure 3. Boxplots of the raw counts for a sample of birds under three different grazing regimes: low (white), moderate (grey) and high (dark grey). Each boxplot shows the mean along with the lower and upper quartiles, which represent the edges of the box. Outlying points are shown extending beyond the whiskers of each plot. The species number is also reported beneath each boxplot

Plots of the raw data for a selection of the species in the dataset reveal that some species are impacted by grazing more so than other species. Moreover, for some species, counts across sites can be quite variable. Figure 3 presents boxplots highlighting the mean abundance and corresponding lower and upper quartiles for six species observed during this study. Extreme values are exhibited by those plots extending beyond the whiskers of the boxplot.

For comparison, we plot the 'pooled' expert opinion Figure 4 for the impact of grazing on this subset of birds. Bars that extend above the dotted line at zero indicate that the experts predict an increase in abundance for that species under that particular grazing level. Bars drawn below the line at zero indicate an expected decline for that species and grazing regime. The precision (rounded) is also reported near each bar to give an indication of the level of agreement between experts.

Of notable interest in Figure 3 is the average increase in numbers of species 11 under high levels of grazing compared to low and moderate levels of grazing—a feature also noted by the experts in Figure 4. The variability in observed counts of species 11 is also evident under high grazing regimes, which may in part explain the lower observed precision among experts ($\tau = 2.221$) compared to other grazing regimes and other species.

Varying abundance of species 6 under the three grazing regimes is also highlighted in Figure 3, with the largest counts on average being recorded under moderate levels of grazing. This is contradictory to what the experts reported in Figure 4, although the precision around their 'pooled' expert belief ($\tau = 1.65$) seems to suggest that there was some disagreement in opinions. Experts do concur however, that this species will decline under high levels of grazing ($\tau = 30$).

Species 9 shows an increase in observed counts (on average) under low levels of grazing, an observation confirmed reasonably confidently ($\tau = 3.97$) by experts in Figure 4. The other three species summarized in Figure 3 show little difference in abundance between the three grazing regimes explored. On the other hand, experts seem to be suggesting major declines for species 18 and 24 under high grazing levels compared to other grazing regimes.

Although interesting, these exploratory results should be interpreted with some caution because of the prevalence of zeros in the data. We may see differences between species at a particular grazing level in exploratory investigations of the data; however, these differences may not be statistically significant once the zeros have properly been accounted for in a model. Furthermore, the incorporation

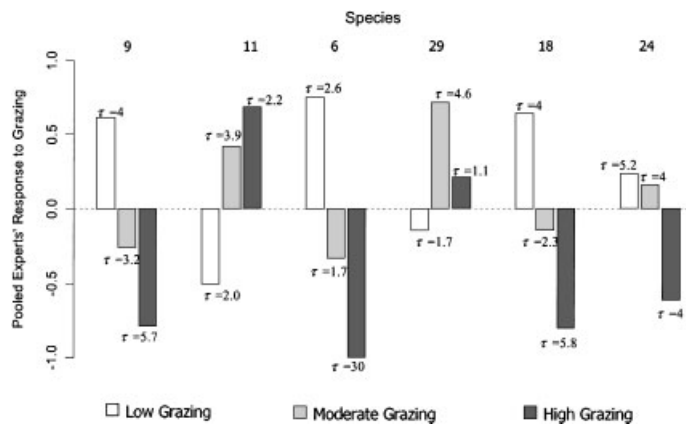


Figure 4. Barplots showing the 'pooled' experts' opinion on bird response to grazing for six species of birds. Each bar shown represents the mean as reported in Table 1, with the precision, τ (rounded), shown near each bar. A line is drawn at zero to represent the combined belief that a species will undergo no change for a particular grazing regime. Bars drawn beneath the line at zero indicate a decline for that species, while bars drawn above the line at zero indicate an increase in abundance. The species number is also reported above each bar

of expert information into such a model may provide clarity about a species and its response to grazing, while for other species it may highlight uncertainties in the data or variations in opinions that need further exploration. These issues are investigated more thoroughly in the following sections of this article.

4.2. Models with no expert information

Results from fitting the observed data to the four models investigated are summarized in Table 2. This table shows the posterior mean, standard deviation and 95 per cent credible interval for the variance components estimated in each model. Estimates of the overdispersion parameter, δ , are also presented in Table 2, where appropriate.

Overall, the estimates are similar with and without modelling explicitly for overdispersion. In addition, the posterior mean estimate for δ is estimated between 0.44 and 0.47, with credible intervals that are significantly less than one, which confirms the lack of overdispersion in the data. Based on this information, results that follow will describe models fitted without the overdispersion parameter.

4.3. Grazing random effect

In Table 2, the grazing random effect estimated for each component of each model explains most of the variation in the data. Compared to the random effect for species in the two-component model, the variance estimated for grazing is nearly eight times larger. Compared to the random effect for species within grazing, the estimated variance component for grazing is approximately four times larger. Variance component estimates in the mixture model have a similar interpretation but are slightly lower in magnitude.

Figure 5 shows how the estimated variance for the grazing random effect was partitioned in the two models. The left y-axis on each plot shows the predictions on the logit and log scales for the

Table 2. Summary of the variance estimates for the four models in the absence of expert information. Results are broken up into the various components fit in each model as shown in (1) and (2). Estimates for the overdispersion parameter, δ , are also provided, where estimated. Statistics presented are the posterior means, standard deviations (SD) and 95 per cent credible intervals (CI)

Parameter	Two-component			Two-component (overdispersion)		
	Mean	SD	95%CI	Mean	SD	95%CI
Presence/absence						
σ_{g0}^2	6.355	26.13	(0.63,29.68)	6.295	32.15	(0.64,29.85)
σ_{s0}^2	0.840	0.84	(0.10,2.13)	0.871	0.53	(0.14,2.16)
σ_{sg0}^2	1.589	0.61	(0.66,2.99)	1.576	0.57	(0.72,2.94)
Abundance given presence						
σ_{g1}^2	4.416	17.78	(0.49,20.77)	4.35	19.71	(0.44,20.13)
σ_{s1}^2	0.569	0.57	(0.22,1.15)	0.717	0.30	(0.29,1.46)
σ_{sg1}^2	0.244	0.10	(0.10,0.49)	0.140	0.09	(0.03,0.36)
Overdispersion						
δ				0.471	0.11	(0.29,0.74)

Parameter	Mixture			Mixture (overdispersion)		
	Mean	SD	95%CI	Mean	SD	95%CI
Absence (structural zero)						
σ_{g0}^2	4.903	20.83	(0.44,23.46)	4.130	14.66	(0.32,20.73)
σ_{s0}^2	1.065	0.66	(0.16,2.66)	1.157	0.76	(0.16,3.01)
σ_{sg0}^2	1.590	0.66	(0.61,3.18)	1.804	0.76	(0.70,3.61)
Abundance (with random zeros)						
σ_{g1}^2	4.281	46.80	(0.43,19.45)	3.940	23.67	(0.36,18.39)
σ_{s1}^2	0.611	0.25	(0.25,1.23)	0.726	0.32	(0.27,1.51)
σ_{sg1}^2	0.280	0.12	(0.12,0.57)	0.189	0.14	(0.04,0.55)
Overdispersion						
δ				0.437	0.10	(0.28,0.67)

components that focus on modelling absences and abundance, respectively. The right y-axis shows the corresponding predictions transformed back on to the probability scale, and for abundance, expected counts are shown.

Figure 5(a) reveals for the two-component model (solid line) substantial variation between grazing regimes, highlighting that the probability of presence of species in general is expected to decline under high rates of grazing and increase under low levels of grazing. Under moderate levels of grazing there is an indication of an increase in the probability of presence, although the corresponding credible interval includes zero (neither an increase nor decrease). In the case of the mixture model (dotted line), results suggest that, under high levels of grazing, a zero count for birds is more likely to be treated as structural, that is, the bird is unlikely to be present, while under low levels of grazing, zero counts are more likely to be treated as random, that is, the bird may exist under a specific grazing regime but may not be seen. This pattern is also observed under moderate levels of grazing but is more tenuous.

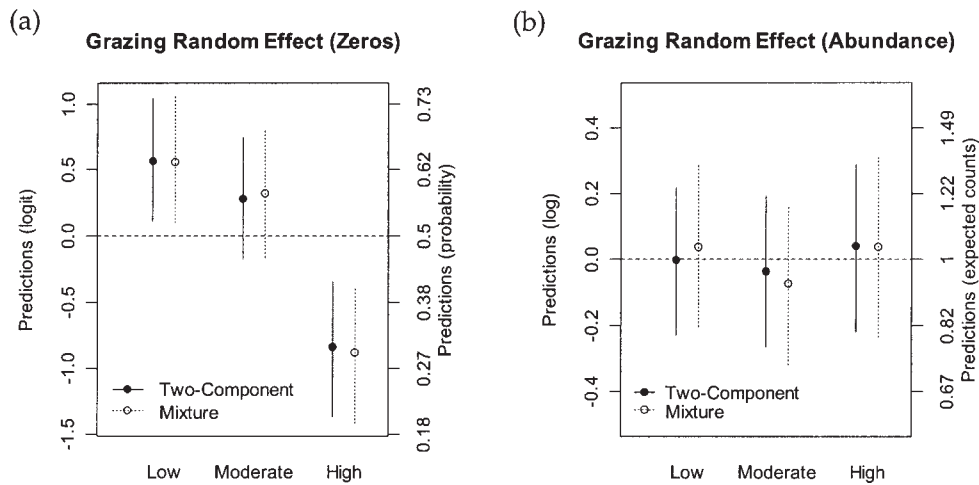


Figure 5. Predictions for the grazing random effect for (a) the component that models the zeros and (b) the component that models abundance for each model that shows how the variance was partitioned across grazing levels. Results from the two-component model are indicated by a solid line, while for the mixture model, predictions are indicated by a dotted line. Posterior means and 95 per cent credible intervals are shown

Figure 5(b) shows the variation in predictions across grazing levels for the component that focuses on abundance for each model. It is apparent that for the two-component model (solid line) there is little difference in bird numbers between grazing regimes, given that the birds are present to begin with. For the mixture model (dotted line), care must be taken with the interpretation of these random effect predictions, since abundance should be interpreted together with whether a zero is treated as structural due to absence or random due to non-detection even when present. These results confirm those of the first model, suggesting that given that a zero count arises through non-detection even if present, bird numbers do not change significantly across grazing regimes. These results are not surprising given that, for short surveys, presence/absence defines most of the variation. For larger surveys, where counts are recorded at lengths longer than 20 min. over larger areas, the abundance of each species could be captured more effectively.

4.3.1. Species random effect. The variance components for the species random effects in all four models are very similar and appear to be slightly higher for those components that model absences compared to those that model abundance. Posterior mean estimates of the variance when absences are the focus is 0.84 and 1.065 for the two-component and mixture model, respectively, with corresponding estimates of 0.569 and 0.611 when abundance is the focus.

Figure 6 displays the predictions calculated from the species random effect fit in the two-component model and shows how the variance for this random effect was partitioned across species. For ease of interpretation, we only discuss the results for the two-component model. Predictions for the species random effect in the mixture model are very similar.

In Figure 6(a), the predictions of the random effect for the presence/absence component of the two-component model highlight only one species (24) having a significant increase in the probability of presence, irrespective of grazing, suggesting that species 24 has a significant deviation from other species in the model. All other species, despite showing slight increases or decreases in the probability of presence, are not significant.

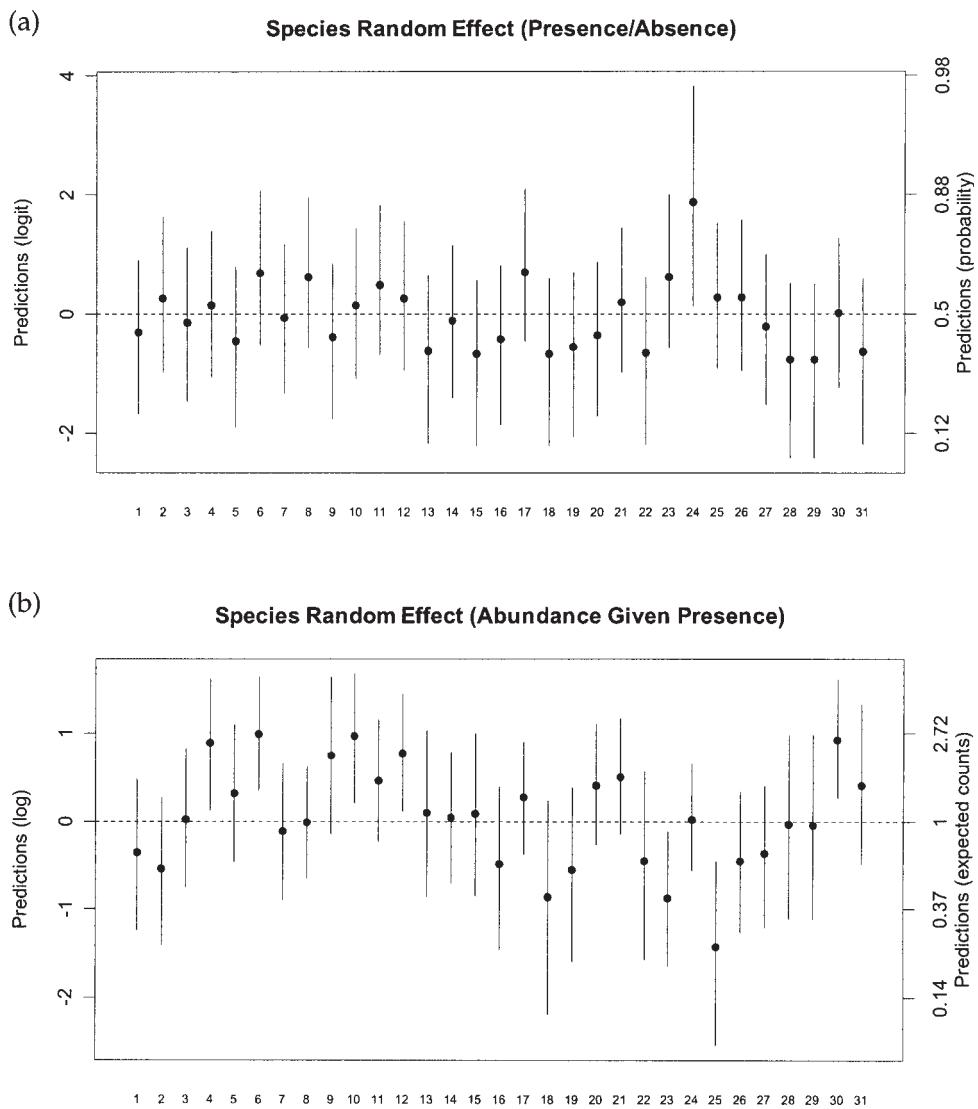


Figure 6. Predictions for the species random effect for (a) the component that models presence/absence and (b) the component that models abundance given presence for each model. Posterior means and 95 per cent credible intervals are plotted

Figure 6(b) presents the predictions of the species random effect for the component that explores abundance, given that a species is present. Note that some species showing a significant increase (decrease) in abundance considering this component alone were not necessarily observed more (less) frequently at one or more grazing levels and/or sites. The results in Figure 6(b) have arisen because of the type of model that we are fitting to take into account the high frequency of zeros. Those species that exhibit zero counts at a particular grazing level have no data with which to model the abundance of the species given presence in the two-component model. This, to some extent is also true for the mixture model. In these circumstances, where there are no data and after accounting for other terms in the

model, the prior in the Bayesian model is used to 'inform' the model and arrive at a prediction for the species. Due to the non-informative nature of the prior as highlighted in (1) and (2), the posterior mean will naturally lie near zero with very wide credible intervals. This type of result occurs for species 3, 13, 15, 28 and 29. Those that are predicted to significantly increase comprise species 4, 6, 10, 12 and 30. Birds which are predicted to significantly decrease in abundance given presence consist of species 13 and 14.

4.3.2. Species within grazing random effect. The random effect for species within grazing reveals a variance estimate larger than that estimated for the species random effect and higher than that estimated for the component that focuses on abundance given presence. This suggests that a higher proportion of the variation is explained by the presence/absence component than in the abundance given presence component. This may be a reflection of the design of the study and associated with differences from modelling presence/absence data as opposed to modelling count data.

Figure 7 summarizes how the variation was partitioned across species within a grazing regime and shows the predictions resulting from fitting these random effects in the model. From an ecological perspective, these results are more interesting because they allow you to observe the impact of grazing on species monitored in the study irrespective of the variation between birds and the variation between grazing regimes. Of the random effect predictions presented in Figure 7(a) for the presence/absence component of the model, three species of bird are predicted to significantly increase with respect to grazing. Species 26 and 2 are expected to increase under low levels of grazing, while species 11 is expected to increase in terms of the probability of presence under high levels of grazing. Species 3 and 31 are suggested to decrease under low grazing but are not statistically significant.

Predictions for the component focusing on abundance given presence are presented in Figure 7(b) and show little variation between species within a particular grazing level, particularly under high levels of grazing. This has largely resulted from lack of data, that is, zero counts recorded for species at a particular grazing level. In circumstances where there are no data, the prior is used to inform the model. Since the prior is fairly non-informative, we cannot expect the predictions themselves to be informative. Moreover, predictions for these species are unlikely to be significant, which is why we are seeing many posterior mean predictions around zero accompanied by very wide credible intervals.

The only species showing significant changes in abundance given presence based on this random effect alone is species 11, which is predicted to increase in abundance given that it is present under high grazing levels and species 12, which is expected to increase when it is present under moderate levels of grazing. A decrease in abundance for this species is highlighted under low levels of grazing, but this result is not significant. A decrease in abundance is also suggested for species 6 under high grazing, while an increase is noted under low grazing; however, these are both not significant.

4.4. Models with expert information

In this section we discuss the case where expert information is incorporated into the models introduced in the previous section using informative priors as shown in (3). Since we showed that there was no evidence of extra-Poisson variation in Section 4.2, we only discuss the two-component model and the mixture model.

Estimates of the variance of each component of the two-component and mixture models are presented in Table 3. In comparison with Table 2, expert information has had a noticeable impact on the variances estimated for each random effect. Moreover, it appears to have provided more structure to the components by tightening up credible intervals in some cases. This is confirmed in Figure 8, in

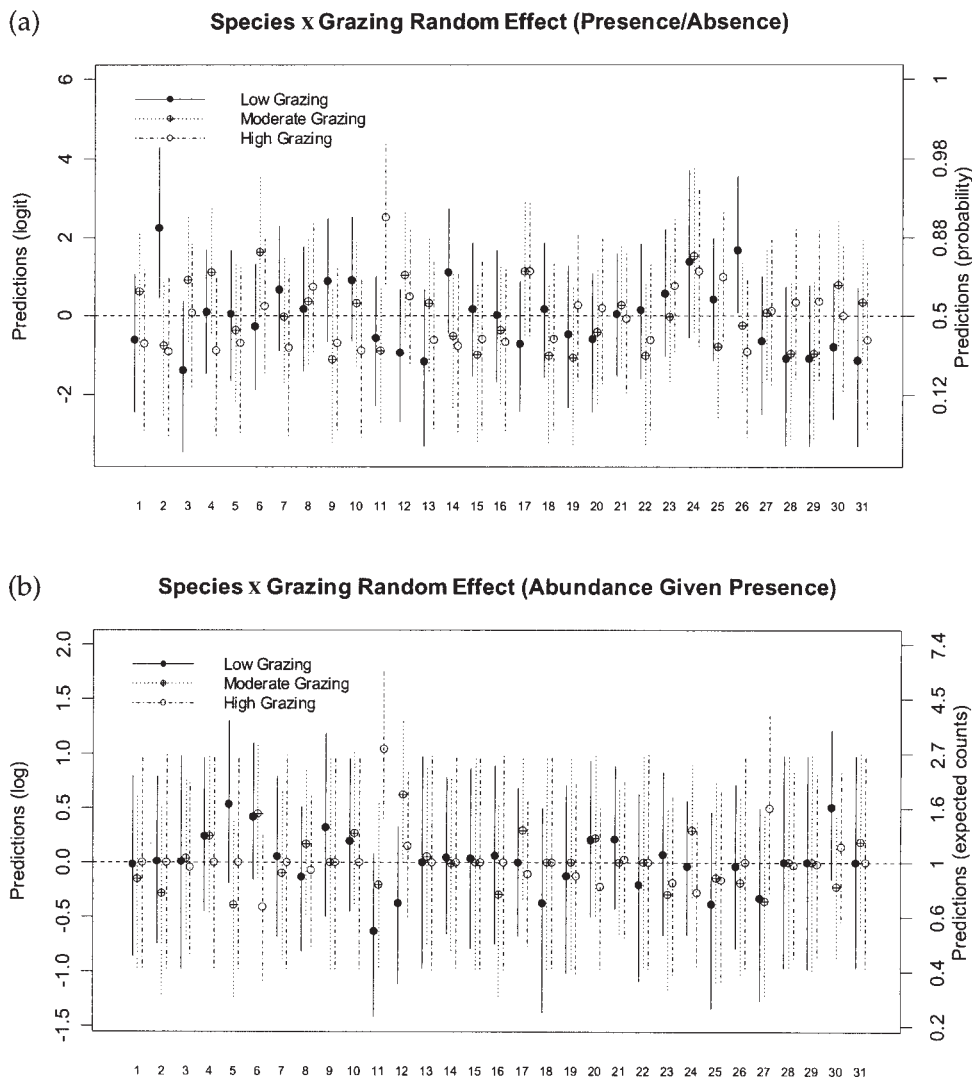


Figure 7. Predictions for the species within grazing random effect for (a) the component that models presence/absence and (b) the component that models abundance given presence for each model. Posterior means and 95 per cent credible intervals are plotted

which the variance estimates for the models with and without expert information are compared. We see that the largest impact has been on the estimate of the variance for the grazing random effect, particularly for the component that models absence in each model (Figure 8a). In previous models that did not include expert information; the grazing random effect explained most of the variability in the data. Given some structure, we see in Figure 8 that most of the variation is being explained by the species within grazing random effect (3.645, CI = [1.30,7.54]) followed by the species random effect (2.591, CI = [0.79,5.62]) and then the effect of grazing (1.112, CI = [0.04,6.75]).

For the component that focuses on abundance for each model (Figure 8b), most of the variation still appears to be explained by the grazing random effect (9.05, CI = [0.56,47.52]) followed by the random

Table 3. Summary of the variance estimates for the two-component and mixture models with expert information. Results are broken up into the various components fit in each model as shown in (1) and (2). Statistics presented are the posterior means, standard deviations (SD) and 95 per cent credible intervals (CI)

Parameter	Two-component		
	Mean	SD	95%CI
Presence/absence			
σ_{g0}^2	1.112	5.98	(0.04,6.75)
σ_{s0}^2	2.591	1.25	(0.79,5.62)
σ_{sg0}^2	3.645	1.58	(1.30,7.54)
Abundance given presence			
σ_{g1}^2	9.050	61.71	(0.56,47.52)
σ_{s1}^2	1.047	0.39	(0.49,1.98)
σ_{sg1}^2	0.334	0.17	(0.11,0.77)
Parameter	Mixture		
	Mean	SD	95%CI
Absence (structural zero)			
σ_{g0}^2	1.119	12.67	(0.04,5.96)
σ_{s0}^2	2.897	1.45	(0.71,6.33)
σ_{sg0}^2	4.047	1.82	(1.41,8.42)
Abundance (with random zeros)			
σ_{g1}^2	8.790	52.44	(0.58,47.18)
σ_{s1}^2	1.047	0.40	(0.48,2.04)
σ_{sg1}^2	0.387	0.21	(0.12,0.94)

effect for species (1.047, CI = [0.49,1.98]) and then the species within grazing random effect (0.334, CI = [0.11,0.77]). Moreover, the variance estimates do not change considerably compared to those presented for the model fitted without expert information. The experts do have an impact on the predictions of the random effect, however, particularly in scenarios where no data were available for a particular species and there was a consensus amongst the experts.

4.4.1. Grazing random effect. Given that we did not explicitly ask experts to comment on grazing alone, we thought it worthwhile to examine results when an informative prior for the grazing random effect was 'derived' from the experts' response.

As highlighted by Figure 8(a), the estimate of the variance component for the grazing random effect in the zeros component of each model has been substantially reduced with the incorporation of expert information, and this is reflected in the predictions of the random effect (Figure 9a). For the component that models abundance (Figure 9b), random effect predictions are similar, suggesting that the power of expert information combined with the survey data is insufficient to detect large variations between grazing regimes. This result is perhaps a reflection of the diversity of species chosen in this study. Note too, that the experts were not specifically asked to comment on grazing alone, but the impact that grazing has on birds. Moreover, the observed results perhaps confirm what we would observe in practice, since the impact of grazing alone, across a diverse range of species, is difficult to quantify.

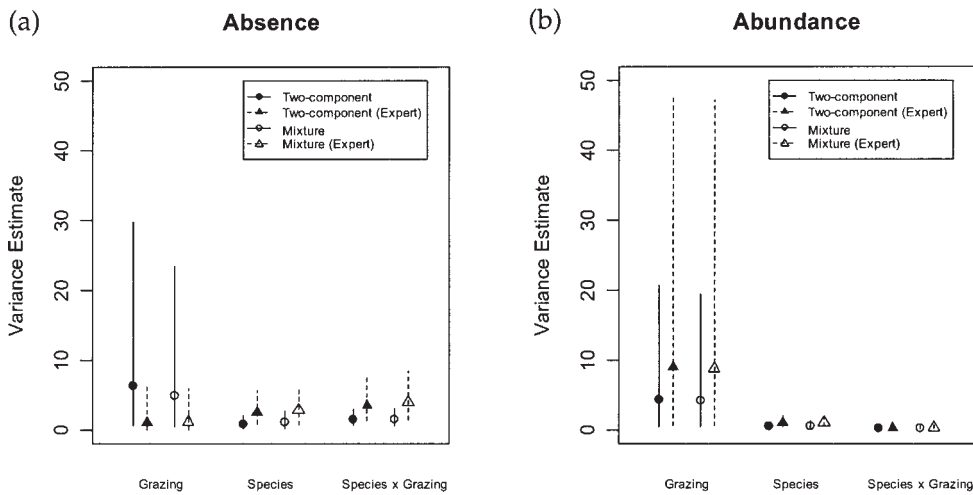


Figure 8. Variance estimates of the grazing, species and species within grazing random effects for the (a) zeros and (b) abundance component of each model

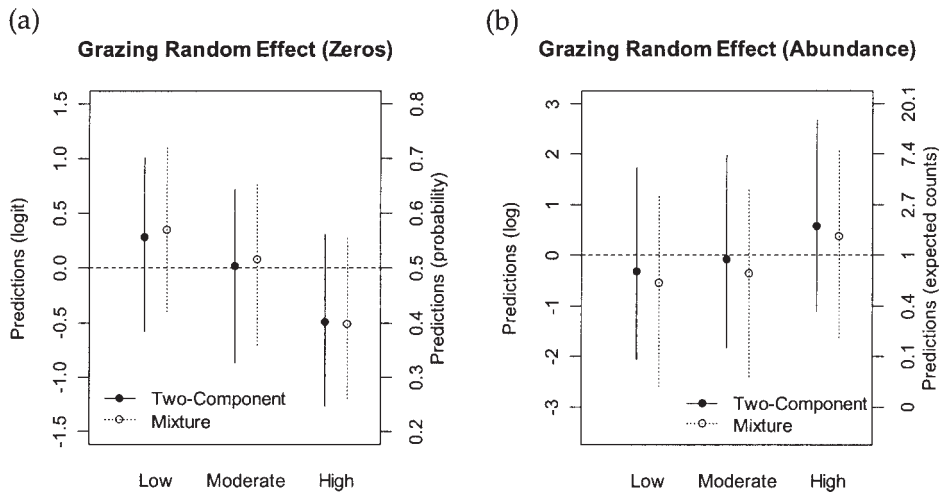


Figure 9. Predictions for the grazing random effect in the presence of expert information for (a) the component that models the zeros and (b) the component that models abundance for each model that shows how the variance was partitioned across grazing levels. Results from the two-component model are indicated by a solid line, while for the mixture model, predictions are indicated by a dotted line. Posterior means and 95 per cent credible intervals are shown

Despite this, there is still a suggestion that under high levels of grazing, birds have a tendency to decline, while under low levels birds tend to increase in terms of the probability of presence.

4.4.2. Species random effect. The variance component estimates for the species random effect have increased with the incorporation of ‘derived’ expert information, suggesting that more variation in the model is attributed to species than in previous models. Note that the priors placed on the species random effect were derived from the expert data, since experts were not asked to specifically comment on the presence/absence or abundance of species in relation to other species surveyed in the study.

Figures 10(a) and 10(b) show how the variation is partitioned across species for the zeros and abundance components, respectively, of the two-component model. Results for the mixture model were similar and therefore will not be presented here. Comparing Figures 6(a) and 10(a) reveal little difference in the predictions apart from a narrower credible interval for the probability of presence of species 24.

Figure 10(b) shows the impact of expert information on modelling the abundance of species given presence. Results look similar to those shown for models without expert information (Figure 6b); however, the credible intervals in some circumstances have been substantially reduced in size. One

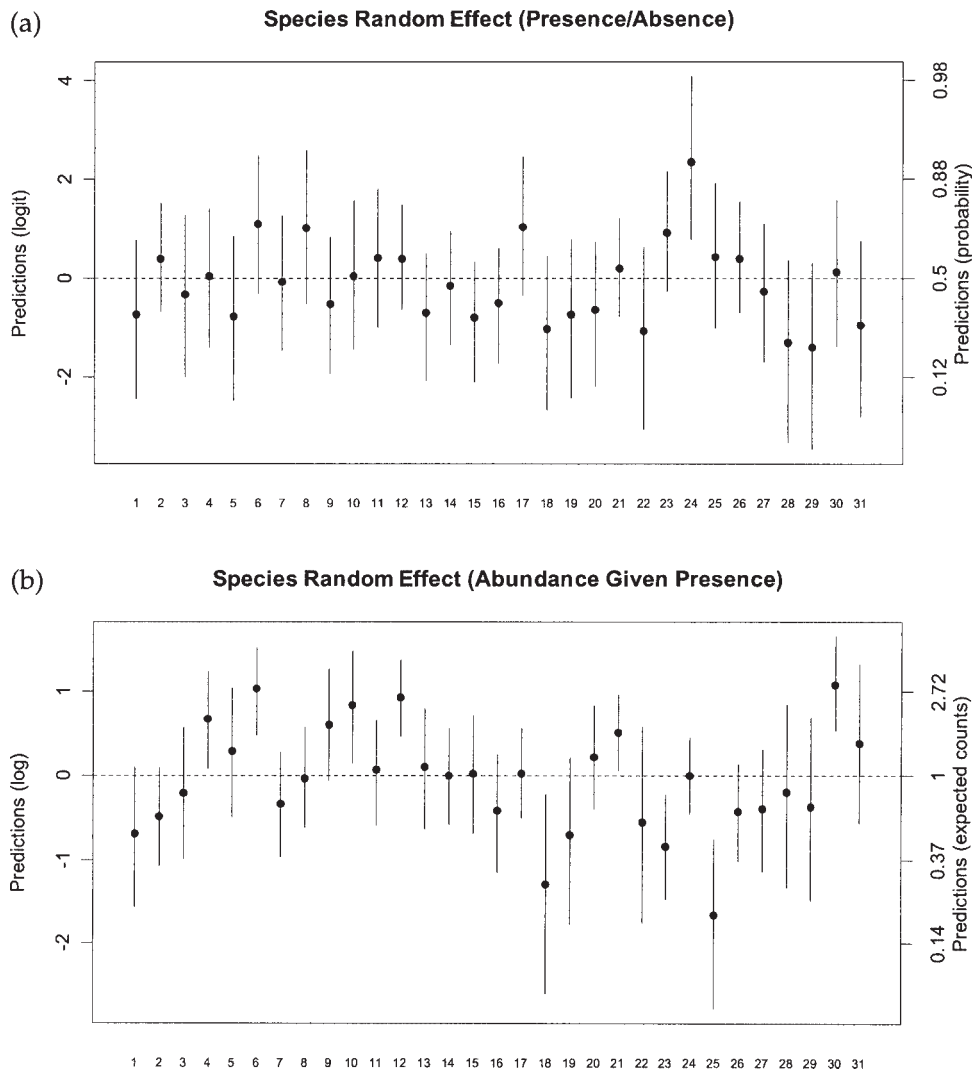


Figure 10. Predictions for the species random effect in the presence of expert information for (a) the component that models presence/absence and (b) the component that models abundance given presence for each model. Posterior means and 95 per cent credible intervals are plotted

additional species (18) is expected to have a decrease in abundance, given presence as predicted by this random effect. Other species (1,2) are suggested to decrease but are not significant, while species 9 is suggested to increase, but again, the credible interval just includes zero.

4.4.3. *Species within grazing random effect.* Predictions for the species within grazing random effect for each component in the two-component model are shown in Figure 11(a) and 11(b), respectively. These plots demonstrate the partitioning of the variance across species within a particular grazing regime.

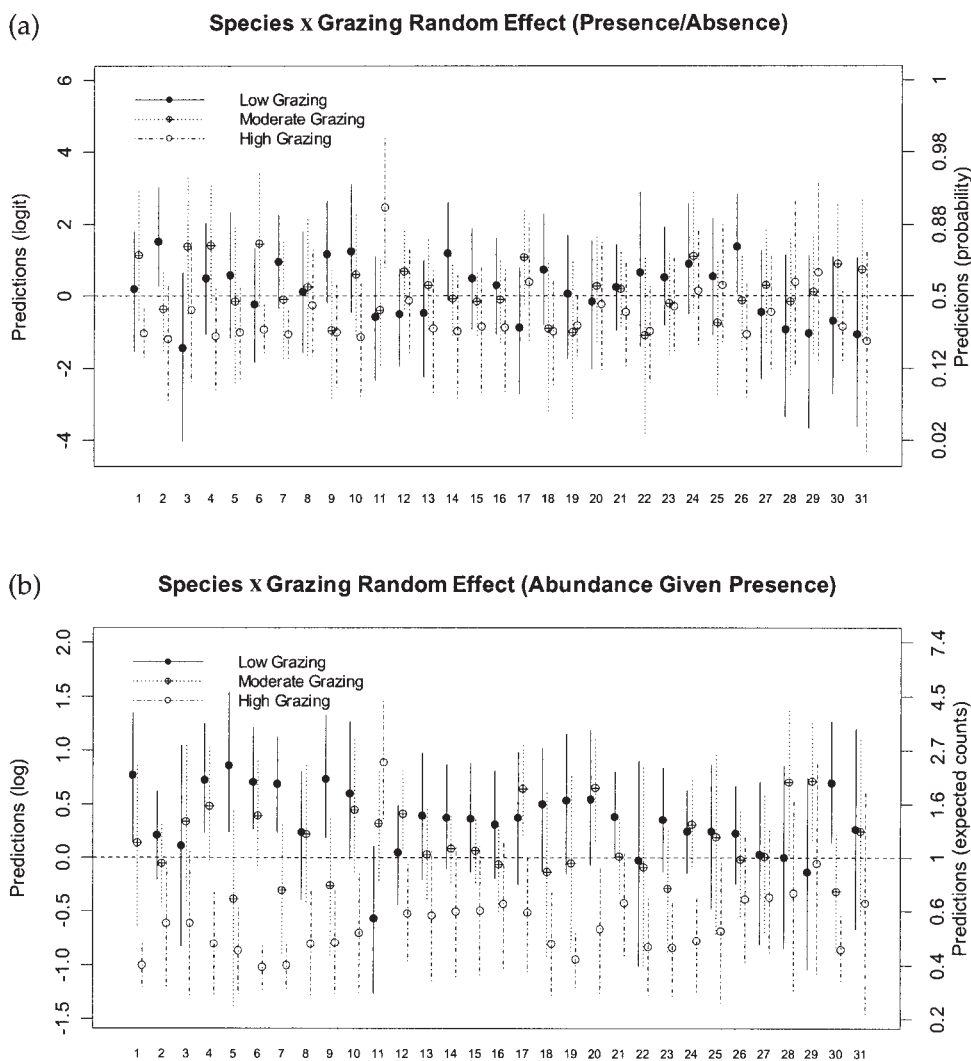


Figure 11. Predictions for the species within grazing random effect in the presence of expert information for (a) the component that models presence/absence and (b) the component that models abundance given presence for each model. Posterior means and 95 per cent credible intervals are plotted

Expert information in the presence/absence component of the model shows some tightening of the credible intervals for the prediction of some species, particularly under high grazing. Moreover, three species (1,6,7) that were borderline significant in the absence of expert information are now significant with the guidance of expert knowledge.

Probably the most outstanding impact of expert opinion can be seen from the predictions presented in Figure 11(b). Figure 11(b) shows the partitioning of the variation across species within a grazing level for the abundance component given the presence of the two-component model. In previous estimates shown in Figure 7(b), many of the predictions were centred at zero with wide credible intervals, reflecting those species with limited data or observed zero counts and essentially implying that these species show no change with respect to grazing. After incorporating expert information, we can visually see how the experts are moderating the data and tightening up the credible intervals in situations where experts collectively were consistent in their knowledge about a species under a particular grazing regime. This is true for the majority of predictions under high grazing levels (1,2,4–10,12,18–20,22–25,30), which for this random effect are all predicted to significantly decrease in abundance given presence. The only species predicted by this random effect to significantly increase given that it is present under high grazing pressures is species 11, a result confirmed by experts since the posterior result is similar to that obtained in the absence of expert information. Under this augmented model, species predicted to significantly increase under low grazing levels consist of 1,4–7,9,21 and 30. Those predicted to significantly increase under moderate levels of grazing include species 12,17,20 and 29. Random effect predictions for all other species, despite suggestions of increases and decreases in abundance, were not statistically significant, suggesting that under different grazing levels these were unlikely to increase or decrease. This is most likely an indication that experts did not concur about the abundance given presence for these species.

4.5. Model checking and comparison of models

We used posterior predictive checks to examine the fit and predictive power of each of the models (without expert information) explored in the previous sections. This type of model checking device has been advocated by Gelman *et al.* (1995) and Congdon (2002), and involves creating independent replicate datasets based on the model fit to the actual data. Once simulated, a test can be performed to see how different the posterior predictions from fitting the model to the simulated data are in comparison to the posterior predictions from fitting the model to the actual data.

Instead of performing an explicit test, we chose a graphical approach to posterior predictive checking using the ideas promoted by Atkinson (1981), McCullagh and Nelder (1989b), Viera *et al.* (2000) and Dobbie (2001). A half-normal plot of the standardized residuals versus the half-normal scores overlaid with a simulated envelope constructed from the minimum and maximum values of the standardized residuals was produced from 19 simulated datasets to provide a baseline reference. Points from the simulated model that lie within the simulated envelope and follow an approximate straight line corresponding to the fit from the actual data indicate a reasonable model fit.

The simulations were produced as follows. We generated 19 datasets simulated using estimates produced from the model fit to the actual data. We fitted each simulated dataset in WinBUGS, discarding the first 10 000 iterations as burn-in and obtained posterior means from the remaining 30 000 iterations. We then found the mean, minimum and maximum values across the 19 simulations, which formed the envelope and plotted it accordingly. We used R (Ihaka and Gentleman, 1996) to construct the simulated datasets, using built-in distributions or those obtained from contributed packages for generating random values from the Poisson, truncated Poisson and negative binomial

distributions. For the truncated negative binomial distribution, we used a rejection sampling algorithm, where we simulated negative binomial random values and discarded zero observations.

Figure 12 shows the results from performing posterior predictive checks for the four models investigated: two-component without an overdispersion parameter (Figure 12a), two-component with an overdispersion parameter (Figure 12b), mixture without an overdispersion parameter (Figure 12c) and mixture with an overdispersion parameter (Figure 12d). We examined these plots for outliers and poorly predicted observations, that is, any points that fell outside the simulated envelopes.

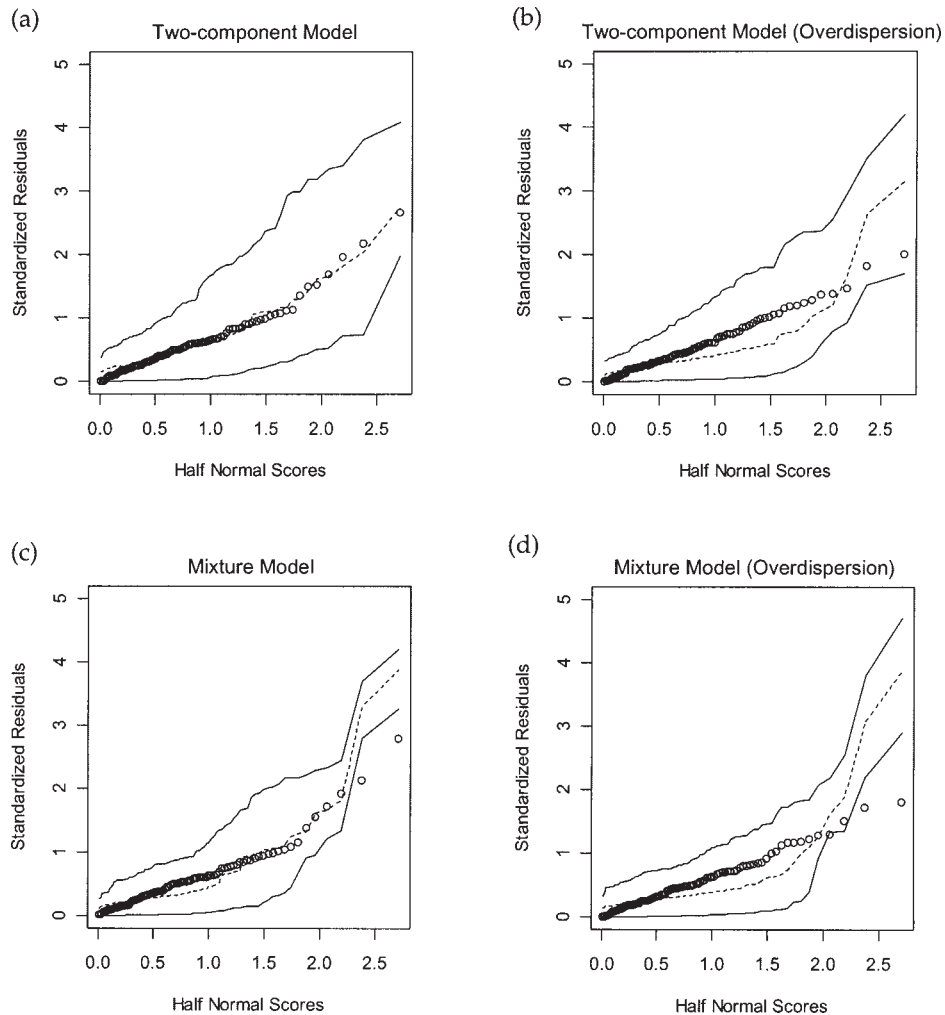


Figure 12. Standardized residuals versus half normal scores for the (a) two-component model without an overdispersion parameter (truncated Poisson), (b) two-component model with an overdispersion parameter (truncated negative binomial), (c) mixture model without an overdispersion parameter (Poisson) and (d) mixture model with an overdispersion parameter (negative binomial). Simulated envelopes were overlayed on each plot. Maximum and minimum values are indicated by solid lines, while the mean is shown as a dotted line overlaying the points

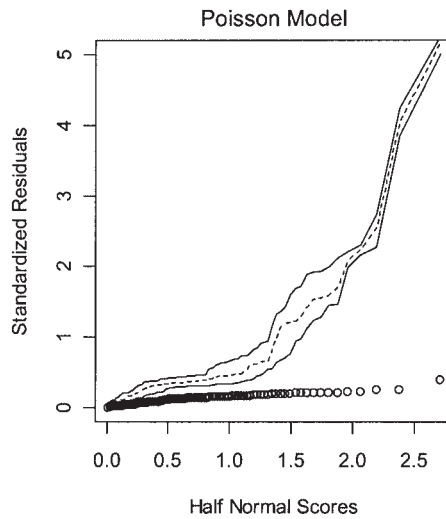


Figure 13. Standardized residuals versus half normal scores for the Poisson model. Maximum and minimum values are indicated by solid lines, while the mean is shown as a dotted line overlaying the points

Plots constructed for the two-component models (Figures 12a and 12b) do not exhibit any influential observations as all points lie within the simulated envelopes. The residual plot for the two-component model where abundance was modelled using a truncated Poisson distribution (Figure 12a) provided a better fit, exhibiting points that followed the mean of the simulated envelope quite closely. Residual plots for the two mixture models (Figures 12c and 12d) identified a couple of ill-fitting points at the extremes, suggesting that this type of model may not be appropriate for these data.

For comparison, we produced a residual plot resulting from fitting a Poisson model to the data (Figure 13). As expected, the plot of the standardized residuals versus the half normal scores indicates an extremely poor fit to the data, which is most likely due to the high frequency of zeros pulling the estimates downwards and therefore biasing results. We also used the deviance information criterion (DIC) (Spiegelhalter *et al.*, 2002) to compare the fit between models and to assess their complexity. Table 4 summarizes the fit for each model. Once again, we computed the DIC for the Poisson model for comparison.

Table 4. DIC values as estimated by the WinBUGS program for five models fit to the bird data without expert information

Model	DIC
Poisson	2845.86
Two-component	
—Truncated Poisson	1780.61
—Truncated negative binomial	1666.08
Mixture	
—Poisson	1779.05
—negative binomial	1672.20

The results show a substantial drop in deviance when we compare the fit of the Poisson model with the four zero-inflated models (approximately 1000 points), indicating that the Poisson model is clearly not appropriate for modelling these data. Of the zero-inflated models examined, the mixture model was slightly superior to the two-component model and the inclusion of an overdispersion parameter led to only a relatively modest drop in deviance.

5. DISCUSSION

We have presented a challenging application of the use of expert opinion to inform us about ecological effects where data are limited. Modelling issues are addressed and elicitation of expert opinion and its incorporation into a model are demonstrated.

The problem considered in this article incorporates information about the impact of grazing on bird abundance elicited from experts in a Bayesian model that accommodates a large number of zero counts. We presented four different approaches to modelling these data to investigate whether bird numbers would decline, increase or stay the same under low, moderate or high grazing pressure for 31 species of birds. Models selected were those that could accommodate the high frequency of zeros in the data and any extra-Poisson variation.

Proposed modelling approaches consisted of the two-component models that modelled the probability of presence of each species and then, conditional on presence, abundance was modelled using a truncated discrete distribution such as a truncated Poisson or truncated negative binomial (for overdispersion), and mixture models that modelled the data using mixtures of Poisson (or negative binomial) and a point mass at zero. Compared to the Poisson model used typically to model count data, these models produced a much better fit to the data when plots of the residual versus half normal scores and the DIC were examined. Diagnostic plots and statistics revealed that the best model for our problem was the two-component model, which modelled abundance given presence using a truncated Poisson distribution.

In this article, we have seen how expert information has moderated the survey data, particularly when little or no data had been collected for a species. In the absence of expert information, we were unable to make any confident statements concerning the impact of grazing on a particular species with the exception of species 11, where it was clear from the survey data that this species had an increase in abundance under high grazing. In the presence of expert information, we noted more structure assigned to the random effects, thus influencing the species within the grazing random effect that was able to inform about how grazing impacts Australian woodland birds, particularly under high grazing levels. This is a result that we would not have achieved in the absence of expert information and it highlights the importance of expert information in a model when data are limited.

Of course, expert information in a model does not always imply that predictions will become clearer or stronger. In some cases, the experts failed to agree, or alternatively, when combined with the survey data, the power to detect significant differences between species within a grazing level was low, therefore resulting in predictions that were similar to those evaluated in the absence of expert information. Just because the estimates are similar with and without expert opinion does not mean disparity between experts. As seen in Section 4, this homogeneity of estimates could be due to other important factors. This impels further research into the source of dissension among experts, an activity outside the scope of the current study.

We presented predictions for each random effect in the model and focused on the species within grazing random effect since the aim of the study was to investigate the impact of grazing on birds in

woodland habitat. Note, we could also have generated model predictions for each of the 31 species of birds investigated in this study. However, from an ecological perspective, these predictions are not very informative as they are obtained with respect to all other species in the model. Given that we have accounted for the variability between species and grazing levels, it is more informative to look at the interaction, that is the variability between species within a particular grazing regime, and make predictions accordingly.

The grazing by species random effect predictions from fitting the two-component model suggests that under the pressures of high grazing, many species of Australian woodland birds are expected to decline, apart from species 11. This supports the theory of Martin and Green (2002), that some species are highly sensitive to changes brought about by intensive livestock grazing. Under low to moderate levels of grazing, there are a number of species that flourish and are predicted to increase in abundance, as highlighted in Section 4. We also noted that some species, in the presence of expert information, showed little change in abundance with respect to the grazing by species random effect. This might be attributed, in part, to the limited data on abundance at a particular grazing level as well as experts disagreeing on the likely response of the species. Species who showed little or no change in abundance under low grazing were species 8, 22, 27, 28 and 29. Species 12 also showed little or no change but its narrower credible intervals suggested that the experts agreed about how this species would behave under low grazing regimes. This was also true for species 7 and 15 under moderate levels of grazing.

Now that we have examined the impact that expert information has on predictions of components in random effects models and how specific species behave under the three grazing regimes, it is worthwhile spending some time discussing what may have caused the high frequency of zeros in the data that led to more complex modelling strategies. We discussed in Section 3 the potential sources of error that may be contributing to the zeros in this dataset and how these can be accommodated in the two-component and mixture models. We pointed out that possible sources of false negative error consist of observer error, design error and 'bird' error in addition to a zero being modelled as structural, that is, absent because there is no suitable habitat. Although we can easily accommodate all three sources of error in one model, due to the nature of the survey design and the way the data were collected, it is difficult to disentangle the design error from the observer and bird error. This presents some interesting issues for future modelling of ecological data that we are currently exploring.

One final issue worth discussing is the elicitation technique used to obtain expert information on birds and grazing. We chose to ask a broad range of experts, located in various parts of Australia, about the impact of grazing on birds. We tried to focus on an approach that would give us a fairly accurate and informative response, was repeatable and would give us a high participation rate because we are aware of the difficulties associated with obtaining information about complex statistical issues from ecologists. One may argue that, in order to comment about the impact of grazing on birds with data recorded at a specific site, the experts would need to have come from the study region or at least be familiar with it. We argue that, in order to make general comments about the impact of grazing on birds, opinions from a broad range of experts is paramount. Eliciting information from one expert would be far more difficult than what was performed for this study, because it requires quantifying a single expert's belief about grazing on birds into a mean and standard deviation that is summarized by a specific probability distribution. By providing a reproducible mechanism for eliciting reliable information from a broad range of experts, we have shown that this can be easily incorporated into a model and extrapolated to provide information about birds in general.

We have demonstrated that it is possible to elicit information from experts and incorporate this information into a model to moderate results. Most importantly, this can be achieved in a framework

using free-ware MCMC software, WinBUGS. The results, although complicated by possible extra-Poisson variation and the high frequency of zero counts, are fairly easy and sensible to interpret. For rare species or when data are limited, expert information becomes a valuable tool that provides structure to a model. Where large scale surveys over long time frames are not practical to perform, expert information provides a cost-effective option for exploring complex issues in ecology.

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REFERENCES

- Agarwal DK, Gelfand AE, Citron-Pusty S. 2002. Zero-inflated models with application to spatial count data. *Environmental and Ecological Statistics* **9**: 341–355.
- Alho JM, Kangas J, Kolehmainen O. 1996. Uncertainty in expert predictions of the ecological consequences of forest plans. *Applied Statistics* **45**: 1–14.
- Arnold GW, Weeldenburg JR. 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.
- Atkinson AC. 1981. Two graphical displays for outlying and influential observations in regression. *Biometrika* **68**: 13–20.
- Barry SC, Welsh A. 2002. Generalized additive modelling and zero inflated count data. *Ecological Modelling* **157**: 179–188.
- Besag J, Green P, Higdon D, Mengersen K. 1995. Bayesian computation and stochastic systems. *Statistical Science* **10**: 3–66.
- Best NG, Cowles MK, Vines SK. 1995. *CODA: Convergence Diagnosis and Output Analysis Software for Gibbs Sampling Output, Version 0.3*. MRC Biostatistics Unit: Cambridge, UK.
- Bohning D, Dietz E, Schlattmann P, Mendonca L, Kirchner U. 1999. The zero-inflated Poisson model and the decayed, missing and filled teeth index in dental epidemiology. *Journal of the Royal Statistical Society, Series A* **162**: 195–209.
- Carpenter SR. 2002. Ecological futures: building an ecology of the long now. *Ecology* **83**: 2069–2083.
- Chatterjee S, Chatterjee S. 1987. On combining expert opinion. *American Journal of Mathematical and Management Services* **7**: 271–295.
- Congdon P. 2002. *Bayesian Statistical Modelling*, chapter 2. Wiley: New York; 17–19.
- Cowles MK, Carlin BP. 1996. Markov chain monte Carlo convergence diagnostics: a comparative review. *Journal of the American Statistical Association* **91**: 883–904.
- Crome FHJ, Thomas MR, Moore L. 1996. A novel Bayesian approach to assessing impacts of rain forest logging. *Ecological Applications* **6**: 1104–1123.
- Dennis B. 1996. Discussion: should ecologists become Bayesians? *Ecological Applications* **6**: 1095–1103.
- Dobbie MJ. 2001. Modelling correlated zero-inflated count data. *PhD thesis*, The Australian National University, Canberra, Australia.
- Dobbie MJ, Welsh AH. 2001a. Modelling correlated zero-inflated count data. *Australian and New Zealand Journal of Statistics* **43**: 431–444.
- Dobbie MJ, Welsh AH. 2001b. Models for zero-inflated count data using the Neyman type A distribution. *Statistical Modelling* **1**: 1–16.
- Faddy M. 1998. Stochastic models for analysis of species abundance data. In *Statistics in Ecology and Environmental Monitoring 2: Decision making and risk assessment in Biology*, Fletcher DJ, Kavalieris L, Manly BFJ (eds). University of Otago Press: Dunedin; 33–40.

- French S. 1985. Group consensus probability distributions: a critical survey. In *Bayesian Statistics 2*, Bernardo JM, DeGroot MH, Lindley DV, Smith AFM (eds). Elsevier, Amsterdam: Netherlands; 183–202.
- Garthwaite PH, Dickey JM. 1988. Quantifying expert opinion in linear regression problems. *Journal of the Royal Statistical Society, Series B (Methodological)* **50**: 462–474.
- Garthwaite PH, Dickey JM. 1992. Elicitation of prior distributions for variable-selection problems in regression. *The Annals of Statistics* **20**: 1697–1719.
- Garthwaite PH, Dickey JM. 1996. Quantifying and using expert opinion for variable-selection problems in regression. *Chemometrics and Intelligent Laboratory Systems* **35**: 1–26.
- Garthwaite PH, O'Hagan A. 2000. Quantifying expert opinion in the UK water industry: an experimental study. *The Statistician* **49**: 455–477.
- Gelman A, Carlin JB, Stern HS, Rubin DB. 1995. *Bayesian Data Analysis*. Chapman & Hall: London.
- Genest C, Zidek JV. 1986. Combining probability distributions: a critique and an annotated bibliography. *Statistical Science* **1**: 114–148.
- Ghazoul J, McAllister M. 2003. Communication complexity and uncertainty in decision making contexts: Bayesian approaches to forest research. *International Forestry Review* **5**: 9–19.
- Hastings WK. 1970. Monte Carlo sampling methods using Markov Chains and their Applications. *Biometrika* **57**: 97–109.
- Heilbron DC. 1994. Zero-altered and other regression models for count data with added zeros. *Biometrical Journal* **36**: 531–547.
- Iglesias RMR, Kothmann MM. 1998. Evaluating expert knowledge: plant species responses to cattle grazing and fire. *Journal of Range Management* **51**: 332–344.
- Ihaka R, Gentleman R. 1996. R: a Language for data analysis and graphics. *Journal of Computational and Graphical Statistics* **5**(3): 299–314.
- Jacobs RA. 1995. Methods for combining experts probability assessments (review). *Neural Computation* **75**: 867–888.
- James CD. 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 AI. Riparian bird communities in relation to land management practices in floodplain woodlands of south-eastern Australia. *Biological Conservation* **100**: 173–185.
- Kadane JB, Wolfson LJ. Experiences in elicitation. *The Statistician* **47**: 3–19.
- Lambert D. 1992. Zero-inflated Poisson regression with an application to defects in manufacturing. *Technometrics* **34**: 1–14.
- Landrum MB, Normand S-LT. 1999. Applying Bayesian ideas to the development of medical guidelines. *Statistics in Medicine* **18**: 117–137.
- Lawless JF. 1987. Negative binomial and mixed Poisson regression. *The Canadian Journal of Statistics* **15**: 209–225.
- Lawrence PA, Stone JJ, Heilman P, Lane LJ. 1997. Using Measured data and expert opinion in a multiple objective decision support system for semiarid rangelands. *Transactions of the American Society of Agricultural Engineers* **40**: 1589–1597.
- Lee AH, Wang K, Yau KKW. 2001. Analysis of Zero-inflated Poisson data incorporating extent of exposure. *Biometrical Journal* **8**: 963–975.
- 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.
- Martin TG, Green JG. 2002. Wildlife and core conservation areas. In *Managing and Conserving Grassy Woodlands*, McIntyre S, McIvor JGM, Heard KM (eds). CSIRO Publishing: Melbourne; 111–142.
- Martin TG, Kuhnert PM, Mengersen K, Possingham HP. (2005). The power of expert opinion in ecological models: a Bayesian approach examining the impact of cattle grazing on birds. *Ecological Applications* **15**: 266–280.
- McConway KJ. 1981. Marginalisation and linear opinion pools. *Journal of the American Statistical Association* **76**: 410–414.
- McCullagh P, Nelder JA. 1989a. *Generalized Linear Models*. 2nd edn. Chapman & Hall: New York.
- McCullagh P, Nelder JA. 1989b. *Generalized Linear Models*. 2nd edn. Chapman & Hall: New York; chapter 12, pp. 407–408.
- McIntyre S, Martin TG. 2002. Managing intensive and extensive land uses to conserve grassland plants in sub-tropical eucalypt woodlands. *Biological Conservation* **107**: 241–252.
- McIntyre S, Heard KM, Martin TG. 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 KM, Martin TG. 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.
- Mengersen K, Robert C, Guihenneuc-Jouyaux C. 2000. MCMC convergence diagnostics: a review. In *Spatial Epidemiology: Methods and Applications*, Elliott, Wakefield, Best, Briggs (eds). Oxford University Press: 393–414.
- Mengersen K, Robert C. 1999. MCMC convergence diagnostics: a review (with discussion). In *Bayesian Statistics VI*, Berger JO, Dawid AP, Smith AFM (eds). Oxford University Press: Oxford; 415–440.
- Musacchio LR, Coulson RN. 2001. Landscape ecological planning process for wetland, waterfowl, and farmland conservation. *Landscape and Urban Planning* **56**: 125–147.
- O'Hagan A. 1998. Eliciting expert beliefs in substantial practical applications. *The Statistician* **47**: 21–35.
- Pearce JL, Cherry K, Drielsma M, Ferrier S, Whish G. 2001. Incorporating expert opinion and fine-scale vegetation mapping into statistical models of faunal distribution. *Journal of Applied Ecology* **38**: 412–424.

- Podlich HM, Faddy MJ, Smyth GK. In Press. A general approach to modeling and analysis of species abundance data with extra zeros. *Journal of Agricultural, Biological and Environmental Statistics*.
- Popotnik G, Guiliano W. 2000. Response of birds to grazing of riparian zones. *Journal of Wildlife Management* **64**: 976–982.
- Roback PJ. 2001. Supra-Bayesian pooling of priors linked by a deterministic simulation model. *Communications in Statistics, Simulation* **30**: 447–476.
- Sattler PS, Williams RDE. 1999. *The Conservation Status of Queensland's Bioregional Ecosystems*. Environmental Protection Agency, Brisbane.
- Schervish MJ. Comments on some axioms for combining expert judgements. *Management Science* **32**: 306–312.
- Sedgwick J, Knopf F. 1987. Breeding bird response to cattle grazing of a cottonwood bottom-land. *Journal of Wildlife Management* **51**: 230–237.
- Soderstrom B, Part T, Linnarsson E. 2001. Grazing effects on between-year variation of farmland bird communities. *Ecological Applications* **11**: 1141–1150.
- Spiegelhalter DJ, Best NG, Carlin BP, Van der Linde A. 2002. Bayesian measures of model complexity and fit (with discussion). *Journal of the Royal Statistical Society, Series B* **64**: 583–640.
- Spiegelhalter DJ, Thomas A, Best NG, Lunn D. 2003. *WinBUGS Version 1.4*. Imperial College & MRC Biostatistics Unit: UK.
- Steffey D. 1992. Hierarchical Bayesian modeling with elicited prior information. *Communications in Statistics, Theory and Methods* **21**: 799–821.
- Vieira AMC, Hinde JP, Demetrio CGB. 2000. Zero-inflated proportion data models applied to a biological control assay. *Journal of Applied Statistics* **27**: 373–389.
- Welsh AH, Cunningham RB, Donnelly CF, Lindenmayer DB. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling* **88**: 297–308.
- Welsh AH, Cunningham RB, Chambers R. 2000. Methodology for estimating the abundance of rare animals: seabird nesting on North East Herald Cay. *Biometrics* **56**: 22–30.
- Yamada K, Elith J, McCarthy M, Zenger A. 2003. Eliciting and integrating expert knowledge for wildlife habitat modelling. *Ecological Modelling* **165**: 251–264.
- Yau KKW, Lee AH. 2001. Zero-inflated Poisson regression with random effects to evaluate an occupational injury prevention programme. *Statistics in Medicine* **20**: 2907–2920.