Prior information reduces uncertainty about the consequences of deer overabundance on forest birds ☆

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ABSTRACT

Prior scientific knowledge inspires ecological research, hypotheses and debate but is rarely used explicitly to formulate predictive models. Bayesian statistics provide a formal way to include informative priors and evaluate their influence on parameter estimates. We use case studies of the influence of overabundant deer on bird species abundance in the Gulf Island, San Juan and Haida Gwaii archipelagos of western North America to demonstrate the utility of informative priors and Bayesian modelling to determine the consequences of overabundance. We found that by including informative priors about deer browsing impacts on bird species from a study undertaken in Haida Gwaii, the precision of estimates from a similar study undertaken in the Gulf and San Juan archipelagos could be significantly increased. Uncertainty about regional ecological impacts underpins many agencies failure to take management actions. We demonstrate here, that informative priors, when used logically and transparently, can be a highly cost effective way to increase understanding of ecological processes. In some cases, it may be the only way to inform decision-making when scarce resources limit support for long term field research or the threat is sufficiently great that immediate action is required. For several bird species examined here, the inclusion of informative priors strengthened the conclusion that their populations were negatively affected by changes in vegetation structure caused by deer browsing. Our findings suggest that deer browsing in these island archipelagos must be managed if the risk of local extinctions among native flora and fauna is to be avoided.

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1. Introduction

Prior scientific knowledge is used implicitly to formulate hypotheses, design research and test existing theory. Yet, examples of the explicit use of prior knowledge to inform models in ecology and improve their predictions are uncommon (e.g., Martin et al., 2005; McCarthy and Masters, 2005). Bayesian modelling facilitates the incorporation of prior information in model formulation. 'Priors' represent our belief about the parameter of interest as summarised through a probability distribution, which may be derived from previously published data or elicited from experts (McCarthy, 2007). Examples of Bayesian modelling highlight the power of informative priors derived from expert knowledge (Mac Nally, 2007; Martin et al., 2005) and published data (McCarthy and Masters, 2005) to increase certainty around key parameter estimates. For controversial environmental issues, such as the management of overabundant herbivore populations, any reduction of uncertainty about impacts is welcome (McShea et al., 1997; Warren, 2011). Managing deer populations is often socially and politically contentious. Scientific guidance on impacts must be clear and unambiguous if agencies are to commit resources to potentially unpopular conservation management actions. In this paper, we draw on two separate published studies on the influence of overabundant deer on bird species abundance on off-shore islands of Western North America to demonstrate the value of using prior information in a Bayesian model to inform managers about the consequences of overabundance.

Bayesian modelling consists of three main components: (1) a prior probability distribution which summarises previous knowledge about the parameters of interest, $p(parameters)$; (2) a distribution representing the probability of the observational data

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given the model parameters, $p(data|parameters)$, often referred to as the likelihood; and (3) the posterior distribution which reflects the probability of the model parameters given the data and prior information, $p(parameters|data)$ (Fig. 1). The mean of the posterior distribution is the weighted average of the prior mean and sample mean of the data. The relative influence of the prior and the data depends on their relative precisions (1/variance) (Kuhnert et al., 2010). In data poor environments, informative priors can be particularly influential (Kuhnert, 2011; Kuhnert et al., 2010; Martin et al., 2005).

Deer populations in North America have recently expanded in numbers due to relaxed predation pressure and changes in hunting regulations and land uses. There is a growing body of evidence that deer affect bird populations (DeCalesta, 1994; DeGraaf et al., 1991; Hino, 2006; McShea and Rappole, 2000) through the regulation of both cover and architecture of understory vegetation (Côté et al., 2004; Crête, 1999; Gaston et al., 2008; Gonzales and Arcese, 2008; Martin et al., 2010; Stockton et al., 2005; Veblen et al., 1989), altered prey abundance (Allombert et al., 2005b; Wardle et al., 2001), and increased exposure to nest predation (Martin et al., 2008). However, management of abundant deer populations is often met with community opposition (Waller and Alverson, 1997). Securing the community support necessary for the successful implementation of management plans that involve control of deer may require unequivocal evidence of the consequences of unregulated deer populations on forest flora and fauna.

We ask here, whether evidence of deer-mediated effects on birds can be augmented using prior information in a Bayesian ecological model. Specifically, we use prior information from Allombert et al. (2005a) who examined the impacts of abundant, introduced black-tailed deer (Odocoileus hemionus) on island songbird populations to help inform a study by Martin et al. (2011) in a similar island system where this same species is endemic but highly abundant due to the eradication of natural predators and near-absence of human hunting pressure (MacDougall, 2008). Both studies lacked temporal replication reporting on a single spring/summer season of sampling, leading us to ask whether augmenting the more recent study of Martin et al. (2011) using informative priors from Allombert et al. (2005a) could improve the power to detect significant trends, where the term "trend" indicates decreases or increases in abundance with increasing deer browsing

pressure. If the trend is significant, it suggests the impact is consistent in two major island archipelagos of the northwest Pacific coast of North America that differ dramatically in climate, forest cover and natural history. In contrast, regional or temporal differences in deer impacts on bird fauna will be highlighted where the inclusion of prior data does not improve the precision of model estimates. By evaluating the consistency of data and prior information, we examine whether the inclusion of prior information can lead to improved inference and potentially influence management decisions where, previously, uncertainty about relative impacts hindered a management response.

2. Methods

We used data from two studies from island archipelagos in western North America that differ dramatically in climate (mean annual precipitation and temperature: 2376 mm and 8.9 °C versus 988 mm and 10.1 °C; Queen Charlotte City, versus Ganges, BC, respectively; (Wang et al., 2012)) and vegetation cover; Haida Gwaii (Allombert et al., 2005a) and the Gulf and San Juan Islands of the Georgia Basin (Martin et al., 2011; Fig. 2). Black-tailed deer (O. hemionus) are the key herbivores in both archipelagos although their history in each differs (Table 1). Deer are endemic to the Gulf and San Juan Islands (Gonzales and Arcese, 2008), but individual island populations probably experienced frequent extinction events related to predator pressure, island size and isolation (Dairmont et al., 2004). In contrast, deer were absent from Haida Gwaii until deliberately introduced in 1878. They subsequently colonised all but a few small, isolated islands (Golumbia et al., 2008). With abundant food resources, absence of predators and mild climate, deer populations grew exponentially until the 1940s after which they stabilised (Golumbia et al., 2008).

In the Gulf and San Juan Islands predation by cougars (Puma concolor) and grey wolves (Canis lupus nubilus) and hunting by indigenous people and then European settlers from the 1800s onwards likely kept deer densities low prior to 1900 (Gonzales and Arcese, 2008; MacDougall, 2008). By the late 1800s early settlers had exterminated cougars and wolves from the islands (Miller et al., 1935; Shackleton, 2000; Tremblay, 2004) and excluded island indigenous communities from their traditional deer hunting grounds (Arnett, 1999). During the last century, deer populations in this area expanded dramatically as human hunting pressure declined due to a reduction in the areas open for hunting, regulations that enforce buck-only hunting and changing human sentiment (MacDougall, 2008; Shackleton, 2000).

Allombert et al. (2005a) and Martin et al. (2011) analysed two separate natural experiments to investigate the impact of black-tailed deer on island songbird populations in Haida Gwaii and the Gulf and San Juan islands, respectively. Allombert et al. (2005a) described the impact of the sub-species Sitka black-tailed deer (O. h. sitkensis) on songbird populations in Haida Gwaii which forms part of the Western Hemlock Biogeoclimatic zone, whereas Martin et al. (2011) described the impact of O. h. columbianus on songbird populations 600 km south, in the Gulf and San Juan archipelago within the Coastal Douglas Fir Biogeoclimatic Zone (Meidinger and Pojar, 1991). Both studies demonstrated that deer browsing would have indirect effects on songbird species through the alteration of vegetation architecture, particularly those dependent on understory vegetation for nesting and foraging. The two studies used the same bird sampling protocol (50 m radius point counts) to estimate the relative abundance of bird species across islands with different levels of deer browsing. On Haida Gwaii point counts were complemented by spot mapping (Allombert et al., 2005a). Within each island multiple sites were sampled with a total of 12 sites across six islands in Haida Gwaii and 150 sites
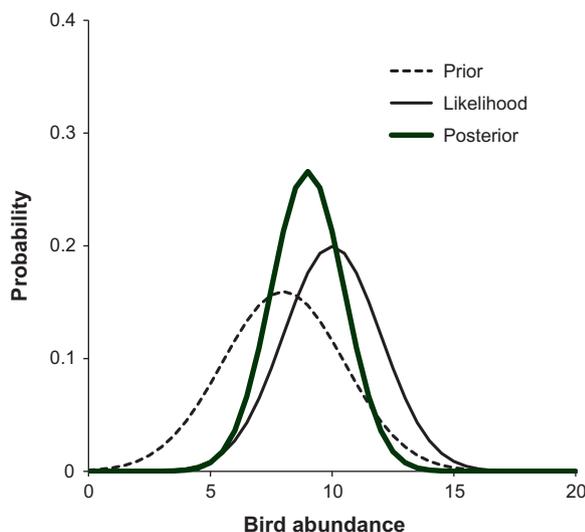

Fig. 1. The prior, likelihood and posterior probability density functions for mean bird abundance. Using an uninformative prior would result in a posterior equivalent to the likelihood. The posterior is more precise than both the prior and the likelihood because it is the weighted average of both.
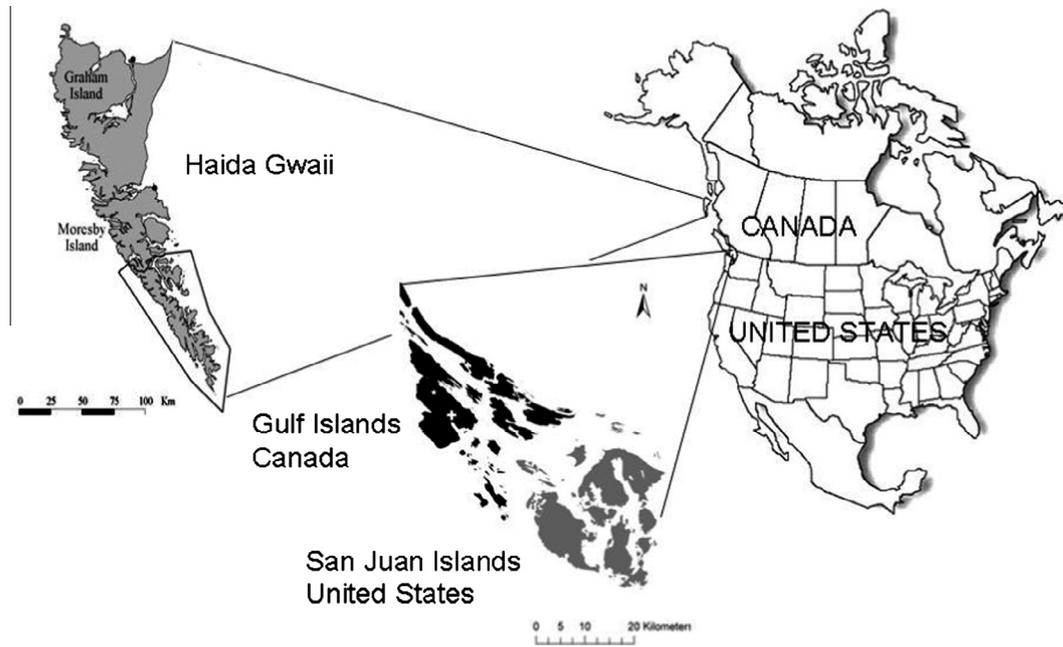
Fig. 2. Location of studies of Allombert et al. (2005a) in the southern section of Haida Gwaii and Martin et al. (2011) in Gulf and San Juan Islands, North America.

Table 1
Classification of deer browsing intensity from two studies of deer impact on birds into low, moderate and high browsing categories used in this study.

Study	Deer Browsing Intensity		
	No/Low	Moderate	High
Allombert et al. (2005a)	No deer present now or historically	Deer introduced <20 years ago	Deer introduced >50 years ago
Martin et al. (2011)	No deer present now or zero or very low density historically	Deer density ranging between 0.1 and 0.5 deer/ha	Deer density ranging between 0.9 and 1.15 deer/ha

across 18 islands in the Gulf and San Juan Islands. Data were collected throughout May and June 1999 in Haida Gwaii and April through June 2007 in the Gulf and San Juan Islands. Two repeat visits were conducted at each site in each study.

Both Allombert et al. (2005a) and Martin et al. (2011) used a generalised linear mixed effects model (GLMM) to estimate the relative abundance of songbird species under different deer histories and densities. In both studies, deer browsing was modelled as a fixed effect and island was modelled as a random effect to account for variation between islands. Allombert et al. (2005a) estimated the density of songbirds across six islands with three different histories of deer browsing: (1) no deer, (2) deer present for less than 20 years, and (3) deer present for greater than 50 years. In the Gulf and San Juan Islands, where deer are endemic, Martin et al. (2011) estimated songbird density across 18 islands grouped into one of three deer density levels: (1) low, (2) moderate, and (3) high based on contemporary estimates of deer density and historical information. Although the deer categories were developed differently in each study, in both studies the intensity of the effect of browsing on vegetation was well correlated with either the duration of deer presence (Stockton et al., 2005; Vila et al., 2003) or the density of deer (Martin et al., 2011) (Table 1). For example, the percent plant cover below 1.5 m on islands with high deer density in Martin et al. (2011) or deer present for greater than 50 years in Allombert et al. (2005a) was remarkably similar. For a complete account of methods used in each study refer to Martin et al. (2011) and Allombert et al. (2005a).

3. Bayesian analysis

We conducted our analysis in three steps. First, we estimated informative priors for the model parameters for bird species that co-occurred in each study for each of three browsing levels using the data and model structure published in Allombert et al. (2005a). To do this, we constructed a Bayesian generalised linear mixture model (GLMM), with browse level as a fixed effect and island as a random effect having non-informative priors with a mean of 0 and precision of 0.001. These posterior estimates formed the informative prior estimates for our subsequent analysis. Second, using the same model structure, we augmented the data from Martin et al. (2011) with the informative priors, to obtain posterior estimates of bird species mean abundance for each browse level. Finally we asked if the uncertainty in the species by browsing estimates of Martin et al. (2011) were substantially reduced through the introduction of informative priors from Allombert et al. (2005a).We fitted a Poisson and negative binomial (NB) distribution to the number of birds of a particular species, y_i recorded at the ith sampling location. We assessed the relative fit of both distributions on model performance using the deviance information criterion (DIC). Results indicated that the fit of the negative binomial distribution was superior and hence results from the negative binomial are presented. The mean, λ_i was represented on the log-scale as a function of deer browsing history: $b_{j(i)}$ (j = low (L), moderate (M) or high (H)) and an island random effect,

l_i. The overdispersion parameter ϕ was gamma distributed (Ga) with shape and scale parameters equalling 0.1. The model was specified as

$$y_i \sim NB(\lambda_i, \phi) \quad (i = 1, \ldots, n.)$$

where

$$\log(\lambda_i) = \beta_L b_{L(i)} + \beta_M b_{M(i)} + \beta_H b_{H(i)} + l_i$$

with priors

$$\beta_j \sim N(\mu_j, \tau_j) \quad (j = L, M, H)$$
$$l_i \sim N(0, \tau_l)$$
$$\phi \sim Ga(0.1, 0.1)$$
$$\sigma_l \sim U(0, 2) \quad \text{where } \tau_l = 1/\sigma_l^2$$

The prior mean μ_j and precision τ_j were normally distributed and resulted from fitting a GLMM to the data of Allombert et al. (2005a) for species that co-occurred in each study. We used the explanatory variable duration of deer presence from Allombert et al. (2005a) as surrogates for low, medium and high deer densities respectively (Table 1). The prior chosen for the island random effect, l_i was Normal (N) with mean 0 and precision τ_l with a uniform prior (U) placed on σ_l (Gelman, 2006).

Sixteen bird species occurred in both the Haida Gwaii and Gulf and San Juan Island studies. The frequency of occurrence of one species, Swanson' thrush Catharus ustulatus was insufficient in both studies to allow reliable modelling, leaving fifteen species for analysis. In each study, authors independently arrived at the same a priori classification of bird species according to their expected susceptibility to deer browsing based on their dependence on understory vegetation for foraging and nesting (Table 2). Six species were classified as strongly dependent on understory vegetation (rufous hummingbird Selasphorus rufous, orange-crowned warbler Vermivora celata, song sparrow Melospiza melodia, fox sparrow Passerella iliaca, Wilsons warbler Wilsonia pusilla, winter wren Troglodytes troglodytes), five as moderately dependent (chestnut-backed chickadee Poecile rufesens, golden-crowned kinglet Regulus satrapa, pacific-slope flycatcher Epidonax difficilis, hermit thrush Catharus guttatus, varied thrush Ixoreus naevius) and four species as having a weak/no dependence on understory vegetation

(brown creeper Certhia Americana, hairy woodpecker Picoides villosus, Townsend's warbler Dendroica townsendi, dark-eyed junco Junco hyemalis).

We assessed the impact of including informative priors on the estimates of deer browsing on songbirds, in two ways. First we compared posterior probabilities of browsing level parameters for each bird species between each browsing level with and without the use of informative priors. Second we assessed whether the trends reported in either Allombert et al. (2005a) or Martin et al. (2011), were different to these posterior estimates when the prior and likelihood were combined. In the comparative assessment, we used the step function in WinBugs to create a Boolean variable that counted the number of Markov chain samples that satisfied the following posterior probabilities: $p(\beta_L > \beta_M)$, $p(\beta_L > \beta_H)$, $p(\beta_M > \beta_H)$, and $p(\beta_L > \beta_M > \beta_H)$. In other words, for the comparison $p(\beta_L > \beta_M)$ we calculated the proportion of simulations in which the low browsing posterior estimate β_L for a given species was greater than the moderate browsing posterior estimate β_M. This calculation was performed with and without prior information. We then compared these two proportions to get an overall measure of the importance of including an informative prior by examining the degree of change in the proportions without and with the prior. These posterior probability comparisons we performed by recording the number of times the difference in the proportions without and with prior information were greater than 20% and 30%. For example, if the proportion of simulations without an informative prior that satisfied the criteria was 0.36 and the proportion with an informative prior was 0.67, the difference of 0.31 was recorded as a >20% as well as a >30% change.

For species predicted a priori to have a strong dependence on understory vegetation we expected a decline in abundance with increasing browsing pressure and therefore the posterior probability comparisons to be high and approach one. In contrast, for species predicted a priori to have a weak/no dependence on the understory vegetation we expected to find no significant change in abundance with increasing browsing pressure and therefore the posterior probability comparison to approach zero. For species predicted to have a moderate dependence on understory vegetation we expected the comparison of posterior probabilities to be greater than 0.5. Species responding negatively or positively to

Table 2
Comparison of bird species posterior probabilities between low β_L, moderate β_M, and high β_H browsing levels with non-informative (Non-inform) and with informative (Inf) prior information. A score of one is given to a comparison where the inclusion of the prior resulted in a shift in the posterior probability estimate by >20% or >30% and are shown in bold.

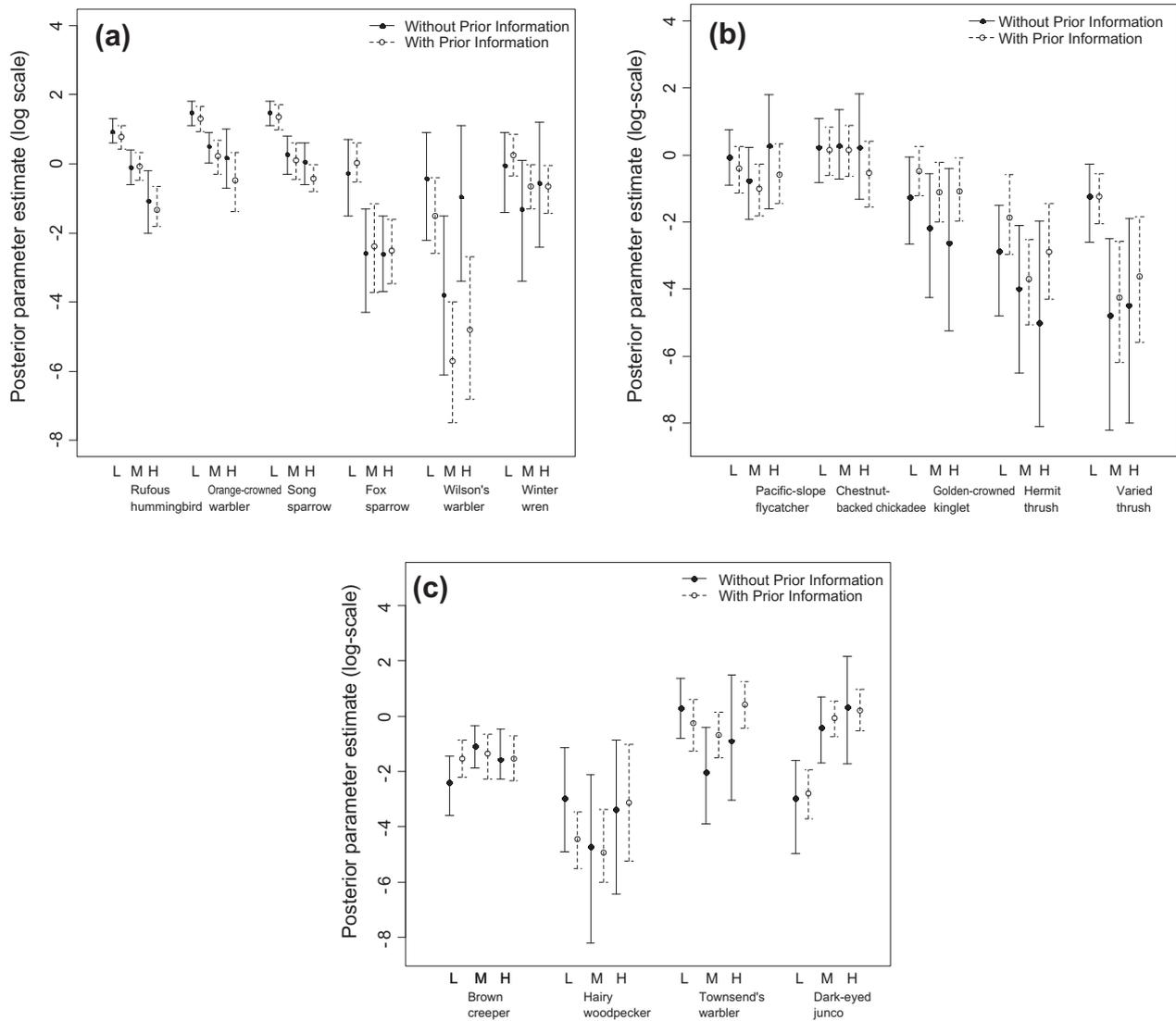| Species	Posterior probability comparisons								A priori dependence on understory vegetation	Change with inclusion of prior	
	$p(\beta_L > \beta_H)$		$p(\beta_L > \beta_M)$		$p(\beta_M > \beta_H)$		$p(\beta_L > \beta_M > \beta_H)$				
Prior	Non-inform	Inf	Non-inform	Inf	Non-inform	Inf	Non-inform	Inf		>20%	>30%
Rufous hummingbird	1	1	1	1	1	1	1	1	Strong	0	0
Orange-crowned warbler	1	1	1	1	0.78	0.96	0.78	0.96	Strong	0	0
Song sparrow	1	1	1	1	0.70	0.78	0.70	0.77	Strong	0	0
Fox sparrow	0.96	1	0.99	1	0.96	0.74	**1**	**0.74**	Strong	1	0
Winter-wren	**0.63**	**0.95**	0.93	0.97	**0.25**	**0.47**	**0.23**	**0.46**	Strong	3	1
Wilson's warbler	**0.41**	**0.96**	**0.72**	**1**	0.21	0.25	**0.19**	**0.40**	Strong	3	1
Varied thrush	0.98	0.99	1	1	0.43	0.32	0.43	0.32	Moderate	0	0
Golden-crowned kinglet	0.86	0.83	0.81	0.86	0.65	0.50	0.54	0.43	Moderate	0	0
Hermit thrush	0.99	0.87	0.82	0.99	**0.99**	**0.20**	**0.81**	**0.20**	Moderate	2	2
Pacific-slope Flycatcher	**0.36**	**0.63**	0.88	0.88	0.14	0.23	0.12	0.20	Moderate	1	0
Chestnut-backed chickadee	**0.52**	**0.87**	0.50	0.49	**0.54**	**0.87**	0.27	0.43	Moderate	2	2
Brown creeper	**0.12**	**0.48**	**0.01**	**0.32**	0.79	0.64	0.01	0.21	Weak	2	2
Hairy woodpecker	**0.62**	**0.12**	0.86	0.74	0.24	0.06	0.21	0.40	Weak	1	1
Townsend's warbler	**0.84**	**0.14**	**0.99**	**0.75**	0.21	0.04	0.21	0.03	Weak	2	1
Dark-eyed junco	0	0	0	0	0.23	0.27	0	0	Weak	0	0
										17/56	10/56

Fig. 3. Posterior parameter estimates (log-scale) of bird species relative abundance and 95% credible intervals for data from Martin et al. (2011) with non-informative priors (closed circle) and with informative priors (open circle) from Allombert et al. (2005a) under three levels of deer browsing intensity; low (*L*), Medium (*M*) and high (*H*) for (a) species predicted to have a strong dependence on understory vegetation and therefore decline with deer browsing, (b) species predicted to be moderately dependent on understory vegetation and therefore show only a moderate trend in decline with deer browsing, and (c) species predicted to show no trend or an increasing trend in relative abundance with deer browsing, based on having low or no dependence on the understory vegetation for foraging and nesting.

increasing browsing pressure in a linear fashion from low to high browsing were expected to have posterior estimates for $p(\beta_L > \beta_M > \beta_H)$ approaching one or zero respectively. Whereas for species responding non-linearly or showing no consistent response to browsing we expected the comparison $p(\beta_L > \beta_M > \beta_H)$ to approach zero.

All models were fitted in WinBugs 1.4.3. (Spiegelhalter et al., 2003) with a burn-in of 10,000 iterations and estimates of the mean and standard deviation of model coefficients and the 95% credible interval monitored for a further 20,000 iterations. Markov Chain Monte Carlo convergence was assessed using standard convergence diagnostics available in the CODA package (Plummer et al., 2006). Throughout this paper, the term 'significant difference' is used in the Bayesian sense to mean that the 95% credible intervals of the estimates do not overlap.

4. Results

Both studies by Allombert et al. (2005a) and Martin et al. (2011) supported the prediction that bird species susceptibility to browsing is correlated with its dependence on understory vegetation. In fact, the raw pattern of bird response to deer browsing was remarkably similar in both studies. The uncertainty in the estimates of Martin et al. (2011) were markedly reduced by formally using the results of Allombert et al. (2005a) as priors. This reduction in uncertainty is illustrated by narrowing of the 95% credible intervals around the species mean estimate for 13 of the 14 species examined under at least one deer browsing level (Fig. 3a–c). The only species whose estimates did not become more precise with informative priors across any browsing level was the orange-crowned warbler (Fig. 3a) which suggests that additional factors are influencing the relative abundance of this species. For six species (fox sparrow, winter wren, Townsend's warbler, dark-eyed junco, golden-crowned kinglet, varied thrush) uncertainty was reduced at all three browsing levels, whereas for a further five species (rufous hummingbird, song sparrow, brown creeper, hairy woodpecker, hermit thrush) uncertainty was reduced at two levels of browsing.

For 30% of the posterior probability comparisons the inclusion of informative priors altered the proportion by >20% and in 18% of comparisons by >30%. For example, for the winter-wren the probability of the posterior estimate under low browsing being
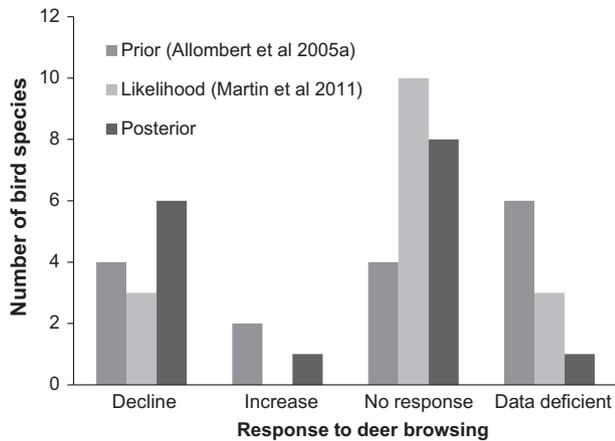
Fig. 4. Assessment of trends reported in Allombert et al. (2005a) (prior) and Martin et al. (2011) compared with results of posterior estimates in the current study. A decline and increase are scored where the trend in bird species mean abundance with browsing intensity was statistically significant; no response is recorded where there was no significant difference (overlapping credible intervals), although there may have been a trend; data deficient is recorded where there were insufficient samples to statistically assess the trend.

greater than under high browsing was 0.63 without an informative prior and 0.95 with an informative prior. Likewise, for the chestnut-backed chickadee, the probability of the posterior estimate under low browsing being greater than under high browsing was 0.52 with a non-informative prior and 0.87 with an informative prior (Table 2).

The most notable difference in our results compared with those of Allombert et al. (2005a) and Martin et al. (2011) concerned four species (Fig. 4). Three species, fox sparrow, Wilson's warbler and varied thrush, exhibited a significant decreasing trend between low and either medium and/or high browsing that was not significant in the previous studies (Figs. 3a and b and 4). Likewise, the dark-eyed junco exhibited a significant increasing trend with browsing (Figs. 3c and 4), not recorded in the previous studies. In total six species were predicted to decline significantly under moderate or high browsing levels, as opposed to four species in Allombert et al. (2005a) and three species in Martin et al. (2011).

The effect of an informative prior was particularly influential on data deficient species. Sample sizes for five species from Allombert et al. (2005a) (hairy woodpecker, dark-eyed junco, hermit thrush, Wilson's warbler and varied thrush) and two species from Martin et al. (2011) (hairy woodpecker and hermit thrush) were low, making inference unreliable in the original studies. While the estimates we derived using informative priors are more precise, we caution that inferences based on informative priors and posterior estimates based on small sample sizes should nevertheless be interpreted with caution (Kuhnert, 2011; Kuhnert et al., 2010).

Overall, six species (rufous hummingbird, orange-crowned warbler, song sparrow, fox sparrow, Wilson's warbler, winter wren) showed a decline in estimated mean abundance with increasing deer browsing as predicted *a priori* (Fig. 3a); only one (varied thrush, Fig. 3b) of the five species predicted *a priori* to be moderately dependent on understory vegetation showed a decline with deer browsing, with the remainder showing little variation across browsing levels. As predicted species with a low dependence on understory vegetation (brown creeper, hairy woodpecker, Townsend's warbler) showed little variation in response to browsing, however, one species (dark-eyed junco) increased with browsing (Fig. 3c and Table 2).

Reduced uncertainty in predictions were most evident for species predicted to decrease with browsing, whereas the greatest variation in the influence of the informative priors was for those

species predicted *a priori* to be least effected by browsing. The random effect 'island' did not account for a notable amount of variation in the data after accounting for the main effects.

5. Discussion

We found that including informative prior information from a study of deer impacts on songbird populations in Haida Gwaii, Canada (Allombert et al., 2005a) reduced the uncertainty in the posterior mean estimates of a similar study conducted 600 km to the south, in the San Juan and Gulf islands (Martin et al., 2011). Using informative priors strengthened the case for deer management in light of the negative impact that high levels of browsing have on several iconic island songbirds (e.g., rufous hummingbird, song sparrow, fox sparrow, orange-crowned warbler, varied thrush). Both Stockton et al. (2005) and Martin et al. (2011) illustrated the profound structural changes in understory vegetation as a result of deer browsing, with the near-complete removal of vegetation between 0.5 and 1.5 m on islands with high levels of browsing. Of the fourteen species we examined, only the dark-eyed junco, a ground foraging, regionally common species, responded positively to increases in deer browsing.

In five cases, the inclusion of informative priors reduced uncertainty in the posterior estimates to such an extent that differences between at least two browsing levels became significant. The inclusion of informative priors strengthened significantly the negative trends in abundance estimated for rufous hummingbird, fox sparrow, Wilson's warbler and varied thrush, and increased significantly the positive trend in abundance for dark-eyed junco. It is precisely this kind of reduction in uncertainty that can lead to better management decisions. For agencies charged with managing forests and their biodiversity, reduced uncertainty about impacts of a native herbivore is likely to be pivotal in garnering support for controversial management actions such as reducing deer density.

In this study we had the luxury of being able to access the original data of Allombert et al. (2005a) to develop our informative priors. In many cases this will not be possible. The minimum required to construct a prior is the mean and some estimate of uncertainty around the mean (e.g., variance, standard deviation, credible interval), as well as the distribution of the data, which are all metrics commonly reported in scientific studies. In cases where the original data are not available or estimates of the mean and variance do not exist, informative priors can be elicited from experts (Kuhnert et al., 2010; Martin et al., 2012a).

Another question that arises when a prior dataset is available, is why not just combine it with the observational data and perform a single analysis? Despite the extra power of a larger dataset, the advantage of keeping the datasets separate is being able to clearly examine whether the trends in the datasets are similar or not. If for example, the trends vary spatially or temporally, combining the datasets would mask this variation. Keeping the datasets separate and undertaking a Bayesian analysis as done here can clearly illustrate the influence of the prior dataset on the observational data. If the trends in each dataset differed, the uncertainty in the posterior estimates with the inclusion of the informative prior, would increase, whereas when trends were similar, the uncertainty would decrease.

The process of updating our understanding of key parameters or the efficacy of management actions and policies based on new information is the foundation of adaptive management (Keith et al., 2011; McCarthy and Possingham, 2007; Walters and Hilborn, 1978). Timely advances in conservation management are more likely to come from such an approach (Chadès et al., 2011; McCarthy and Possingham, 2007). The posterior estimates presented here

can become the informative priors for future analyses on the impact of deer on Western North American bird fauna. The use of posterior estimates as informative priors in successive models, should lead to improved parameter estimates over time.

In contrast, concern over the use of informative priors in Bayesian ecological models (e.g., Dennis, 1996; Lele and Allen, 2006) stems from the potential of priors to overwhelm posterior estimates. Previous studies suggest this can happen when the prior is relatively informative and the data are not (e.g., little data with high variance) (Kuhnert et al., 2010). In addition, the way in which 'priors' are included in the model, that is, either directly as done here, or indirectly through a re-scaling of the likelihood (e.g., Martin et al., 2005), influences the magnitude to which the prior informs the data and resulting posterior estimate (see review by Kuhnert et al., 2010). While much care needs to be taken to ensure prior information is used in a transparent and sensible manner, the alternative of ignoring prior information is inefficient when resources are scarce and decisions are required urgently, as is often the case in conservation planning and management. In our study, the inclusion of prior information confirmed and strengthened the negative impact of moderate and high levels of browsing by deer on several bird species, leaving managers with little doubt about one mechanism contributing to regional declines in these bird species.

Underlying the concern of parameter bias is the notion that every impact in every place is different and therefore that using priors from one region to inform another could lead to biased conclusions about relative impact. In contrast, we found the impact of overabundant deer populations on bird faunas in two different regions to be strikingly similar. The requirement to prove every impact in every region is clearly unachievable. Moreover, the rate of biodiversity loss will in many cases outpace our ability to document the cause of every decline through research, which emphasises the need to develop robust methods to develop models and make predictions (Carpenter, 2002). While we are constantly improving our knowledge through the collection and assimilation of new information, decades of formal ecological studies and expert knowledge already provide precious insights into the impacts of habitat loss and fragmentation (e.g., Mac Nally et al., 2000), fisheries management (e.g., Pauly et al., 1998), livestock grazing systems (e.g., Martin et al., 2005; Martin and Possingham, 2005), invasive species impacts (e.g., Mooney and Hobbs, 2000) and impacts of climate change (O'Neill et al., 2008) on a variety of ecosystems and species. We present an example here to demonstrate how researchers can use such information in a transparent manner to test the transferability of knowledge between regions and ecosystems to improve management predictions and guide conservation practice.

Although prior information cannot replace well-replicated long-term studies and experimentation, there are many situations where its use can inform our field studies and experiments, help refine otherwise uncertain results, and add value and insights that might otherwise be missed. In particular, land management agencies paralysed by a lack of region specific knowledge have the opportunity to use prior information to inform management decisions and act adaptively, rather than take no management action. The decision to wait for more information may be expensive in the long term, as is the case with endangered species, where a high risk of extirpation requires that management decisions be made quickly (Martin et al., 2012b).

Uncertainty about local ecological impacts should not be used as an excuse for lack of management where relevant prior information is available. If priors are constructed with the same level of rigour and logic used to collect new empirical data, they will enhance our predictive capacity, rate of learning and the subsequent speed of implementing conservation management actions.

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