Biological Conservation 165 (2013) 10–17

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

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

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ARTICLE INFO

Article history:
Received 4 October 2012
Received in revised form 18 May 2013
Accepted 21 May 2013
Available online 20 June 2013

Keywords:
Bayesian GLMM
Bird conservation
Black-tailed deer
Gulf Islands
Haida Gwaii
Informative priors
Odocoileus hemionus
Posterior probability
San Juan Islands

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.

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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0006-3207/$ - see front matter © 2013 The Authors. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2013.05.017

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.

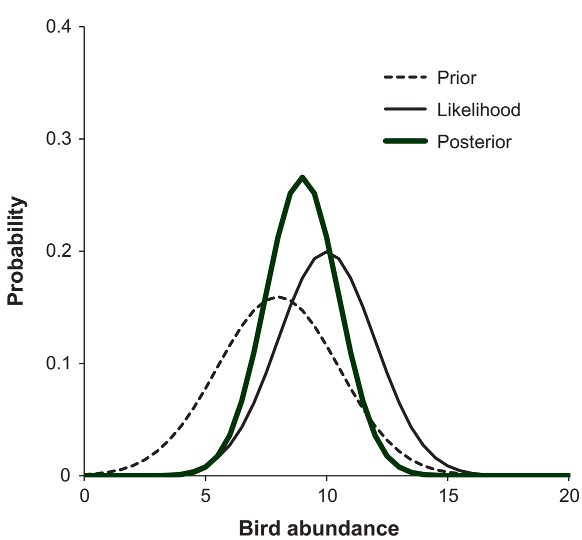

Fig. 1. The prior, likelihood and posterior probability density functions for mean bird abundance. Using an uninformative prior would result in a posterior equivalent to the likelihood. The posterior is more precise than both the prior and the likelihood because it is the weighted average of both.

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 Biogoeclimatic 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