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PERSPECTIVE

Interpreting habitat distribution models of an elusive species, the marbled murrelets: a response to Burger and Page

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Abstract Burger and Page (this volume) evaluated our models of habitat preferences and breeding success of a threatened seabird, the marbled murrelet (*Brachyramphus marmoratus*), based on the largest available set of confirmed nest-sites found in coastal old-growth forest of the Pacific North-West. We believe our study documented novel and unexpected patterns of landscape-level distribution of marbled murrelets in both heavily logged and relatively intact old-growth landscapes and provided insights into how these patterns influence their reproduction, and, eventually, management. Considering the importance of the issue and to ensure appropriate and responsible use of the information we welcome discussion, detailed scrutiny and evaluation of our original results. Burger and Page claim to have identified flaws with model interpretation, data quality, statistical approaches, presentation and interpretation of our results that would invalidate our conclusions. We respond that most of their critique is irrelevant and/or misdirected with respect to our study and the interpretation of GIS data models, and that valid aspects of their claims do not critically affect our conclusions.

Keywords *Brachyramphus marmoratus* · Distribution modelling · Habitat management · Logistic regression · Marbled murrelets · Old-growth forest

Introduction

Using the largest available dataset of 157 confirmed nest locations, we determined suites of variables that co-vary with the distribution and an index of nesting success of marbled murrelets (*Brachyramphus marmoratus*) within the old-growth stratum at two sites in British Columbia, Canada (Zharikov et al. 2006). To our knowledge, this study is the only peer-reviewed publication that used a true used versus available design to derive habitat preferences for the species. Many of our conclusions fell in line with expectations from previous reports (Meyer and Miller 2002; Meyer et al. 2002; Peery et al. 2004; Zharikov et al. 2007). However, some findings ran counter to

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previous research and contemporary beliefs about marbled murrelet habitat selection (Burger and Page, this volume, henceforth "Burger and Page"). Recognizing the importance of the situation we welcome discussion, scrutiny, independent evaluation of our results and model validation. Burger and Page's critique identified several problems, which in the authors' opinion raise doubts about our methods and results and consequently invalidate our conclusions. We conclude that their scrutiny has detected a few valid methodological limitations and instances of imprecise wording, but that the thrust of their critique is misdirected and that our conclusions stand. Burger and Page summarised what they perceived as problems with our original study under five headings. We respond below to each of their comments and then place our response in a broader context.

Interpretation of multiple logistic regression models

Burger and Page suggest that our reporting of results from multiple regression models is misleading since we have interpreted model parameters individually. We respond that multiple logistic regressions are the work-horse of wildlife distribution modelling (Seoane et al. 2004; Vaughan and Ormerod 2005; McPherson and Jetz 2007). Their use is ubiquitous enough to make readers appreciate that impacts of individual variables are implied after controlling for other included predictors—this follows directly from the additive nature of these models. Individual interpretation and/or listing of important variables from multiple logistic regressions is commonplace in applied ecology literature (Meyer and Miller 2002; Meyer et al. 2002; Gibson et al. 2004; Mao et al. 2005; Betts et al. 2006).

Burger and Page suggest that our models have "very low predictive power" based on the low reported Cox R^2 values. Cox R^2 does not describe "predictive power" but rather the percent reduction in deviance due to a given set of independent predictors. This statistic is affected by prevalence as well as the number of predictors (e.g. Johnson et al. 2004a report highly predictive models with Cox R^2 of 0.07–0.12). Predictive (or discriminatory) power of logistic regression models is their ability to discriminate between random positive and negative cases (Pearce and Ferrier 2000). There are several ways to assess it, including r_s statistic (Boyce et al. 2002; Johnson et al. 2004a, b), as, on suggestion of a referee, we did for our habitat selection models. Alternatively, predictive power can be estimated from the area under the curve (AUC) of the receiver operating curve (ROC) (McPherson et al. 2004) as we did for the breeding success models. The r_s and AUC values we report suggest that our models, particularly those for Desolation Sound, are "useful" (cf. Johnson et al. 2004a, b for r_s; Betts et al. 2006; McPherson et al. 2007 for AUC).

Species perception of space, spatial resolution, positional accuracy and edge effects

Burger and Page raise several distinct issues under the heading of "Inappropriate spatial resolution": species perception of space, spatial resolution of geographic data, positional accuracy of geographic and bird distribution data and edge effects.

Species perception of space

Burger and Page imply that our analyses involve inappropriate assumptions about marbled murrelet perceptions of space. Doubtless, inappropriate spatial resolution in modelling wildlife-habitat relations can be a "major impediment" for successful modelling. Habitat sampling should be done at the scale (grain) that is perceived by the study organism or is otherwise relevant to the and e56]TJ53(e56ut-544.741cD18 0 0

definition of edges and patches, as defined by mapped forest cover, roads and streams—the best available GIS data commonly available to both wildlife researchers and habitat managers. The “apparent discrepancy” in patch density between Desolation and Clayoquot Sounds is easy to resolve (see the methods and Fig. 2 of the original paper). Clayoquot has almost three times as much forest per unit area as Desolation. With similar densities of linear features (streams and roads) Clayoquot is thus bound to have more patches, as we defined them, per unit area than Desolation.

Patch size selection and biological significance

Patch size selection

Burger and Page reject our conclusion that murrelets were disproportionately nesting in patches of smaller size at Desolation Sound. We constructed an explicit test of the null hypothesis that murrelet nests were distributed proportionately to the area covered by different patch sizes, allowing for the theoretically continuous distribution of sizes. At Desolation Sound, the patch size distribution of nest sites was statistically non-random. The strongest pattern in the distribution is overusage retically

non-random. The strongest pattern in the

modelling is not about “univariate differences”. It is about quantifying realised environmental niches using predictors likely to exert direct or mitigated effect of species distribution and/or fitness (Vaughan and Ormerod 2005; Whittingham et al. 2006). Neither referees nor Burger and Page considered our predictors irrelevant to the distribution and/or fitness of marbled murrelets. The “means” we provide aid in interpretation of the results. Specifically they show more clearly the direction and relative strength of a particular effect. Whether the differences between mean values of used and random locations appear “trivial” or “significant” is secondary to the fact that marbled murrelet distribution and/or breeding success co-vary with topography and/or distance to the landscape features included in the models.

Biases, mistakes and relevance of other studies

Biases

Burger and Page raise the issue of biases. Bias represents a systematic deviation from a true central value due to a particular factor, whose effect of the response is over- or underestimated. Burger and Page identified potential sources of random noise in our data, but we fail to see any “biases”. We are not claiming that there cannot be any biases with our (abundance and probability of occurrence) represent

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