

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

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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

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 way it selects its environment (Huettmann and Diamond 2006). Since we did not have an a priori knowledge of the scale at which marbled murrelets perceive or select their habitat, we chose a distance-based analysis that would not restrict us to any particular scale (grain). Rather than being a weakness, our approach may elucidate the spatial scales at which the species responds to its environment.

Spatial resolution of geographic data

Burger and Page further imply disparate and inappropriate resolution of our spatial data. Our spatial data came from several raster and vector sources with

broadly similar resolution. To define the old-growth forest layer we used standard 1:20,000 forest cover maps with the minimum mapped unit of ca. 0.1 ha (i.e. ca. 30×30 m). The coarser 1:250,000 dataset referred to by Burger and Page was only used to extract glacier, subalpine and ocean layers and itself is based on 30×30 m satellite imagery. Clearcuts were updated using 30×30 m satellite imagery. Elevation and slope were derived from a 25×25 m Digital Elevation Model. Nine-cell (3×3 neighbourhood) averaging referred to by Burger and Page is not re-sampling—it does not make the resolution coarser, it makes the data smoother.

Positional accuracy of geographic and bird distribution data

Burger and Page raise an issue about positional accuracy of our data. Any positional error introduces random noise into the data, not a particular bias. Reese et al. (2005) showed that logistic regression models based on random sampling strategies (as employed by us) are robust to the levels of random environmental error of up to 50%. Visscher (2006), cited by Burger and Page, indeed reported strong influence of location error on habitat selection models in fragmented landscapes. His study, however, addressed misclassification of the preferred habitat type (probability of its selection by a moving radio-collared animal), which tended to bias habitat selection in habitat-specialists towards appearing more general. We employed an approach where location error introduced random noise, not a directional bias and therefore, Visscher's results are not applicable to our work.

While no explicit information on positional accuracy of our land-cover data was available, experience in the field and elsewhere suggests that it is of the same order of magnitude as resolution (i.e. few 10 s of meters). The coarser 1:250,000 database, used to extract glacier, subalpine and ocean layers, will have lower positional accuracy, but average distances from nest locations to the features derived from this database were large (5–6 km) making the effect of extra random noise in the data inconsequential. Bradley et al. (2004) estimated positional accuracy of nests located from a helicopter to a maximum of 100×100 m. We did not cite Bradley et al.'s (2004)

statement about the accuracy of nest locations because we further adjusted nest locations beyond those used by Bradley et al. (2004). Huettmann et al. (in preparation), based on differential GPS measurements, state that the resultant accuracy was <30 m. Finally, 37% and 78% of nests at Desolation and Clayoquot, respectively, were ground-located giving them the positional accuracy of ca. 10 m.

These points notwithstanding, we agree with Burger and Page that we over-reported the precision of distance variables and model parameter coefficients. However, lower precision, would add random noise, but not bias our analyses in an obvious way. Since all of our average point-to-feature distances were at or greater than 100 m, our results would have remained as they are had we applied a coarser resolution.

Edge effects

Burger and Page argue that our approach and scale were inappropriate to measure direct “edge effects”. We agree, and did not attempt to investigate the edge effects themselves, i.e. effects of edge-to-interior gradients in the strength of particular biological or physical phenomena. Instead, as stated “We test whether the choice of a nest site and breeding success co-vary with the size of the nest patch and Euclidean distances to landscape features likely to produce ‘edge effects’...” (Zharikov et al. 2006). Thus, birds nesting in an area with more clearcuts, even if it is several kilometres across, were hypothesised to experience an overall greater clearcut edge effect and this is the question that we addressed in the study. Thus, this criticism is misdirected.

Use and interpretation of fragmentation and patch size data

Burger and Page suggest that our definitions of patches is incorrect because it does not reflect what murrelets perceive as “patches” and because we have a higher patch density in what is typically acknowledged as less fragmented habitat. Again, we did not make any assumptions about the scale at which marbled murrelets perceive their environment. However, we did provide an explicit and tractable

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 at the low end of the patch size distribution, at patch size 10 ha and then a weaker positive selection at 200 ha (Fig. 1). Further in support of our claim, this analysis already excluded the 25% of our sample found in patches too small to have been mapped (see “Mistakes”, below).

Based on a restatement of these data in Fig. 3 of Zharikov et al. (2006), Burger and Page point out that pooling the data at the 210 ha threshold would produce no patch size preference, but this is arbitrary; one could bin data at many thresholds to produce or obscure patterns, which is why we tested the entire continuous distribution.

Burger and Page argue that we have emphasised the Desolation Sound results at the expense of the Clayoquot analyses. The “observed vs. expected” comparison for Clayoquot Sound appears negative for patch sizes below ca. 210 ha (cumulative area 50,000 ha), but we failed to find significant deviation from random expectation. This failure may indeed be due to limited power from the smaller Clayoquot Sound sample size. As stressed by Burger and Page,

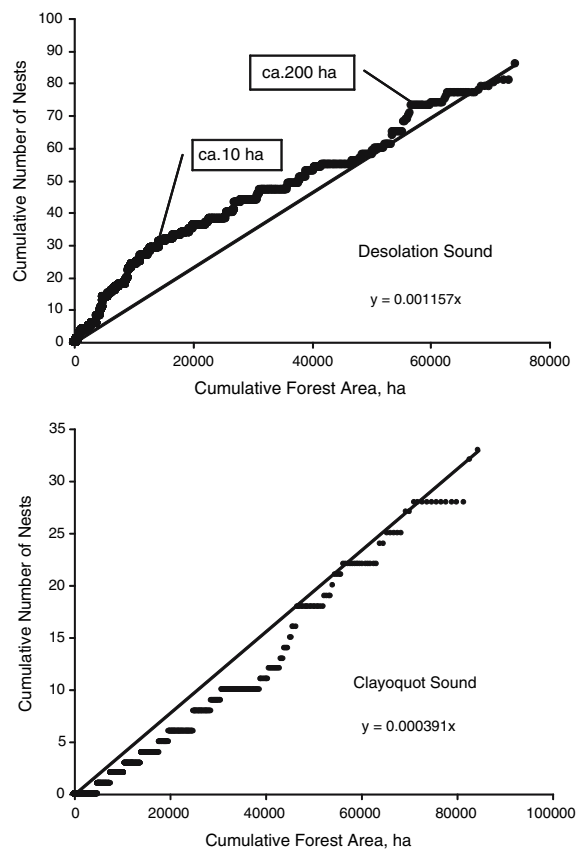


Fig. 1 Cumulative plots of area under old-growth forest and the number of marbled murrelet nests encompassed. The linear trend represents a neutral selection for patch size ($p_i = c\alpha_i$). Boxes indicate the individual fragment sizes with the greatest deviation from the neutral trend (erratum from Zharikov et al. 2006, Fig. 2, which, due to a production error, omitted the expected distribution line for Desolation Sound)

our results with respect to patch size selection may differ between Desolation and Clayoquot Sounds, and our overall conclusion in the discussion is that “patch size is neither a consistent nor an important nesting habitat predictor in this species”; it is thus safe to say that the birds nest throughout patch sizes. This statement reflects both our results and the current state of knowledge of habitat selection in the species.

Biological significance

In their “Overemphasis” section Burger and Page state that “univariate differences were the foundation of our discussion and conclusions”. The statement clearly misrepresents our work. Distribution

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 approach (e.g. McFarlane Tranquilla et al. 2005), but we do contend that Burger and Page have not detected any.

Our data came from two areas in south-western British Columbia: one heavily logged and the other relatively intact. Burger and Page are correct in noting that we put more trust into Desolation Sound models, primarily because the Desolation dataset is three times larger than the Clayoquot dataset and it should produce more robust distribution models (Reese et al. 2005; Vaughan and Ormerod 2005). Whether or not our Desolation Sound models are applicable elsewhere depends on whether the Desolation dataset captures a sufficiently broad range of environmental conditions, so as to be representative of conditions at other sites, and whether there are more “Desolation” or “Clayoquot” Sounds across the species’ range. To answer the first point—our more recent paper (Zharikov et al. 2007) already suggests that the environmental range covered by the

Desolation dataset is sufficient to predict murrelet distribution between the two sites within south-western British Columbia, although more testing and validation is desirable. The second query requires region-wide classification of coastal old-growth landscapes and landscape forecasting, which would help resolve the potential applicability of all results throughout our region.

Mistakes

Burger and Page chide us for claiming that finding 25% of nests in unmapped small pockets of old-growth at Desolation Sound supported our conclusion, based on the analysis of mapped patches, that disproportional usage occurred in small patches at Desolation Sound. They are correct that due to a lack of data on the availability of such small pockets, we cannot know whether this usage deviates from random, and this was technically a misstatement on our part. However, the overuse of “smaller patches” stands regardless of what falls outside of the mapped old-growth cover. Had we defined the availability of the smallest patches, and we could have found (1) overusage, in which case *D*-max would have peaked at an even smaller patch size, (2) proportional usage, in which case our result would have remained as presented, or (3) underusage, in which case the curve over the range currently plotted would still peak at 10 ha which is less than what is traditionally suggested for murrelets.

Relevance to other studies

Burger and Page are “troubled” by the way we cited other relevant papers. We cite conventional papers in our introduction and develop our initial hypothesis, not all of which were subsequently upheld, based on these papers (p. 108). Generally, the previous peer-reviewed research has shown that measures of abundance of the murrelets are positively correlated with the amount of old-growth. These results, however, are not directly relevant to our study—abundance and probability of occurrence do not have to be and sometimes are not correlated (Nielsen et al. 2005). The same can be said about breeding success (Pidgeon et al. 2003). These two variables

(abundance and probability of occurrence) represent two distinct responses of animals to their habitat—selection and amount of use. Here we dealt only with selection. In our discussion we could not, nor did we wish to discuss every possible source available on the species for a number of reasons—particularly because no other marbled murrelet distribution study is directly comparable to ours.

Conclusions

Burger and Page emphasise that our recommendations are in some respects at variance with existing recommendations of the Canadian Marbled Murrelet Recovery Team (CMMRT) and British Columbia government policies, and state that they are concerned that the conclusions we reached could be used to justify alternative management approaches with respect to patch size. We agree, but see this, potentially, as progress towards a sustainable science-based management, rather than an abandonment of “precautionary” conservation principles.

The recommendations of the CMMRT derive from the huge literature on ground-based assessments of murrelet distributions. Ground-based observations cannot be made in much of the rugged topography around Desolation Sound, thus much previous literature is biased with respect to this site. Although such influence of topography may be of minor importance over much of the range the species that has been previously studied, it may be quite relevant further north in British Columbia and along the southern and central Alaska coastline, which forms the heart of the species’ distribution.

Wildlife management often consists of efficient tradeoffs, approved by the public. In British Columbia, a real tradeoff faced repeatedly by those harvesting coastal old-growth forests containing marbled murrelet nesting habitat, and those charged with approving cutting plans, involves defining areas set aside for the birds. In homogeneous swaths of superb habitat, creation of large areas may be the best approach. Where habitat is patchy, e.g. fragmented by clearcuts or terrain topography and hydrology, artificially mandating creation of larger areas could result in inclusion of substantial portions of less preferable habitat. Given the murrelet’s propensity for nesting at low densities, and their reluctance to pack into areas, there may be

circumstances in which smaller and more widely dispersed patches will support more birds than fewer larger patches. Such an approach could be misused by planners, and those charged with management need to be appropriately cautious. We are not advocating the creation of small patches as a primary strategy for keeping marbled murrelets common, widespread, and abundant, but our results suggest consideration of situations in which such an approach may be one component of an overall strategy for doing so.

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