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PERSPECTIVE

The need for biological realism in habitat modeling: a reinterpretation of Zharikov et al. (2006)

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Abstract Zharikov et al. (2006: Landscape Ecology 21:107–120) modeled the nest-site habitat use of marbled murrelets (*Brachyramphus marmoratus*) in Desolation Sound (DS) and Clayoquot Sound (CS), British Columbia. They compared known nest sites, located with radio-telemetry, with randomly-located points within the same areas. Their conclusions suggest that murrelets tended to nest in disproportionately smaller fragments within the more disturbed DS landscape; streams, steeper slopes, and lower elevations were selected in both landscapes; murrelets nested closer to recent clearcuts than would be expected in the DS landscape; and survivorship of nestlings was greater in areas with recent clearcuts and was positively correlated with recent habitat fragmentation. These conclusions are contrary to current management guidelines in British Columbia, and therefore require close scrutiny. Our detailed examination reveals flaws in their use of data, application of modeling, and most seriously, interpretation of the results. Problems include: conceptual errors in the interpretation of models; inappropriate spatial resolution; confusing use and interpretation of fragmentation and patch size data; overemphasis of statistically significant but biologically trivial results; and ignoring some contradictory studies. We conclude that it would be risky to apply the results from Zharikov et al. in the selection of murrelet nesting habitat for management purposes in British Columbia. Our review identifies issues that may arise in other ecological modeling studies and stresses the need for biological realism in addition to statistical rigour.

Keywords Ecological modeling · Biological realism · Habitat use · Nest site selection · Marbled murrelet · *Brachyramphus marmoratus* · British Columbia

Introduction

Multivariate models and multi-modeling techniques (e.g., Burnham and Anderson, 2002) are essential requirements to understand the often complex, multidimensional factors affecting habitat use and habitat selection by animals (Manly et al. 2002). Mobile organisms seldom respond to a single stimulus or requirement when selecting breeding habitats, making management difficult when these habitats need to be clearly identified in the face of conflicting human demands. Consequently, sophisticated models have been developed with the aim of improving habitat management and conservation (Manly et al. 2002; Beissinger et al. 2006). Most models cannot include all the variables likely to affect habitat selection and the selection of data and interpretation of the resultant

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models needs to be solidly grounded in biological reality (Beissinger et al. 2006). If this is not the case then apparently successful models that meet certain statistical thresholds might be incorrectly interpreted, and if applied to management, this could lead to the application of measures that actually harm the organism being managed.

A recent modeling exercise by Zharikov et al. (2006) was undertaken to identify parameters that might be important for predicting forest habitat used by nesting marbled murrelets (*Brachyramphus marmoratus*) in British Columbia, Canada. This small seabird (Family Alcidae) is listed as threatened in Canada and in the states of Washington, Oregon and California, largely because of reductions in its nesting habitat in old seral coastal forests (Nelson 1997; McShane et al. 2004). Reliable identification and prediction of nesting habitat is particularly important in British Columbia, because not all habitat that might be used by murrelets is likely to be set aside due to the high value of this land for forestry. The habitat that is selected by governments and the forest industry to be maintained for marbled murrelets should therefore include the critical micro-habitat features (e.g., platform limbs and canopy gaps) needed by nesting murrelets (Canadian Marbled Murrelet Recovery Team 2003; Province of British Columbia 2004).

There have been several earlier attempts to develop habitat algorithms and heuristic models to identify murrelet nesting habitat in British Columbia, with mixed success (reviewed by: Tripp 2001; Burger 2002). The approach taken by Zharikov et al. (2006) was the first to compare actual nest sites, located using radio telemetry, with randomly selected points within the surrounding landscape. The study used nest sites from two study areas, Desolation Sound (DS) on the southern mainland, and Clayoquot Sound (CS) on the southwestern coast of Vancouver Island. Because of substantial differences in vegetation, climate, and topography, these two areas were treated separately by Zharikov et al. (2006).

Zharikov et al. (2006) reached strong conclusions on the distribution of murrelet nests relative to patch size, distance to forest edges and effects of other landscape-level variables. Some forest managers within British Columbia may be tempted to interpret this study as justification for establishing habitat reserves that are small (considerably smaller than 200 ha), fragmented by clearcut logging, and biased towards steep slopes. This approach would be contrary to the precautionary guidelines of the Canadian Marbled Murrelet Recovery Team (2003) and the provincial Identified Wildlife Management Strategy (Province of British Columbia 2004) that recommend establishing a wide range of habitat patch areas, avoidance of hard-edges created by clearcut logging, and treating slope as a neutral variable. Our detailed examination of Zharikov et al. (2006) reveals flaws in the use of data, application of modeling techniques, and most seriously, interpretation of the results from the models. This paper outlines these problems, leading to the conclusion that it would be premature and risky to apply the results from Zharikov et al. (2006) in the selection of nesting habitat for management purposes in British Columbia.

The problems with Zharikov et al. (2006) fall into five, somewhat overlapping categories: (1) conceptual errors in the interpretation of models; (2) inappropriate spatial resolution; (3) faulty use and interpretation of fragmentation and patch size data; (4) overemphasis of statistically significant but biologically trivial results; and (5) ignoring potential biases in the data and modeling approach. These general categories are outlined below, including re-examination of some of the conclusions reached by Zharikov et al. (2006). In a broader context, our analysis identifies problems that could arise in other habitat modeling studies when there is insufficient emphasis on realistic biological interpretations. This is an issue that needs to be considered by both habitat modelers and the wildlife managers who apply such models

Conceptual errors in the interpretation of models

Recognizing the intricate inter-relationships among the range of habitat variables likely to affect murrelets, Zharikov et al. (2006) used a multi-modeling procedure (Burnham and Anderson 2002) that tested numerous combinations of these variables. The models deemed most successful at separating nest sites from randomly located points contained 4–7 habitat variables. Implicit in this modeling procedure is the understanding that it is the *combination* of these co-variates that best explains habitat use. This is particularly relevant when the variables are intercorrelated, as many were in this study. Unfortunately, the authors ignore this almost completely in their abstract and discussion, and instead focus on univariate interpretations of the co-variates selected by the models. We are told, for example, that in logged landscapes (i.e., DS), murrelets nest closer to recent clearcuts than would be expected. As discussed below, a univariate test of the distance-to-edge data would almost certainly reveal no differences between nests and random sites. What would be more accurate is to say: "In combination with the effects of elevation, slope and proximity to streams and glaciers, murrelets showed some affinity for hard edged clearcuts, relative to randomly selected points, at spatial scales exceeding 1 km". Managers could then apply the findings with the appropriate combination of variables instead of following incorrect and simplistic univariate conclusions.

Most of the models constructed by Zharikov et al. (2006) provide very low predictive power. As these authors recognized, R^2 values in logistic regressions comparing known habitat with random points are likely to be low, and they considered values of 0.2–0.4 to represent a good fit. Most of the models produced in their analysis failed to reach even this modest standard of predictability. Their "best" models for describing habitat selection in murrelets at both DS and CS had R^2 values of 0.115 (p. 113); i.e., 88.5% of the likelihood of separating nests and random points was not explained (assuming that Zharikov et al. used the Cox method for deriving R^2 for maximum likelihood models). The model selected to explain nesting success in DS performed moderately better ($R^2 = 0.227$). Alternative techniques used in the paper for testing predictive capacities did indicate better predictive abilities of the best models, but these were not adequately explained so that managers could appreciate the level of predictability. For example, the best models for predicting nest site selection in DS (models 9 and 12) had Spearman rank correlations of 0.893 and 0.811, respectively, in cross-validation tests. This does not necessarily imply a corresponding accuracy in predicting habitat use, however, because these were the correlations within 10 probability bins, the details of which were not provided. All the indicators (R^2 values and cross-validation correlations) suggested low predictability for the CS models. From these weak models, Zharikov et al. (2006) reach strong conclusions that are at risk of being accepted as biologically important by forest managers.

Inappropriate spatial resolution

The use of inappropriate spatial resolution for testing ecological processes is a major impediment to the success of predictive models (Huston 2002). Related issues for models based on remotely observed data are errors in location (e.g., location of nests in this case) and mapping errors (e.g., edges and patch boundaries). Such errors can cause misclassifications of species-habitat interactions, especially in fragmented landscapes (Visscher 2006), and should be explicitly addressed in landscape models (Hunsaker et al. 2001). There are serious discrepancies between the spatial resolution at which Zharikov et al. (2006) present their results and the resolution of the data that they used to derive these results, and sources of error in spatial locations and patch boundaries were not discussed.

Of the 121 DS nest sites identified by telemetry only 45 nest trees were located and presumably mapped with high precision, but the bulk of the nests were apparently mapped using the helicopter-based telemetry signals and a GPS. The number of nest trees accurately located in CS was not given in the paper. The spatial precision of the helicopter-located nest sites in DS was never tested in the field but was estimated to be within a 100 m × 100 m area (Bradley and Cooke 2001; Bradley et al. 2004). Additional resolution issues arise from the type of habitat data used. The Landsat imagery used had a resolution of 30 m × 30 m and slope angle was estimated by averaging over 75 m × 75 m areas. The 1:250,000 Baseline Thematic Mapping used for forest cover by Zharikov et al. (2006) is similarly coarse-scale and in our work with this database we have regularly encountered polygon boundary errors of 200 m or more. Ignoring the coarse spatial resolution of their raw data, Zharikov et al. (2006) estimated distances from nests to the nearest forest edges with a resolution of 10 m and slope at 1°. Clearly such precision is unrealistic. Had the authors correctly used a coarser resolution that matched their data, most of the differences between nest and random points, and the strong conclusions based on these differences, would disappear (see below).

In the Pacific Northwest, edge effects due to increased predator densities and microclimatic changes in the forest canopy are generally found to extend 50–150 m into the forest from "hard-edge" clearcut boundaries (Chen et al. 1993, 1995, 1999; Brosofske et al. 1997; Kremsater and Bunnell 1999; Masselink 2001). Edge effects at natural forest boundaries, such as streams or avalanche chutes would extend for shorter distances into the forest. Most analysts of marbled murrelet breeding success have considered "edges" to be within 50 m, or at most 200 m, of forest boundaries (Nelson and Hamer 1995; Manley and Nelson 1999; Marzluff and Restani 1999; McShane et al. 2004). The putative benefits of edges to marbled murrelets in providing easier flight access to nest platforms in the forest canopy are unlikely to extend beyond 1–2 tree heights (i.e., 50–100 m at most). To rigorously test edge effects on marbled murrelets one should therefore focus on the 50–200 m bordering the forest edge. Coarser-scale analyses will not reveal edge effects.

As shown above, the spatial resolution of the raw data used by Zharikov et al. (2006) was not fine enough to test edge effects. Furthermore, the closer proximity to edges of nests, relative to random points, which Zharikov et al. (2006) repeatedly emphasize, occurs at a spatial scale 10 times larger than one would expect edge effects to occur (mean distances of nests to edge range from 1.72 to 2.49 km; see Tables 2 and 3 in Zharikov et al. 2006).

It is our contention that coarse-scale satellite imagery and forest cover mapping lack the spatial resolution to adequately test effects of patch size and forest edges on marbled murrelets. Nest sites located by telemetry and mapped using GPS from a helicopter should also not be used for such analyses. It is not surprising therefore, that a fine-scale ground-based analysis of the same DS nest sites by Bradley (2002) produced different results to those of Zharikov et al. (2006). Bradley (2002) analysed nest success from 37 accessible nest sites in DS, using 50 and 100 m scales. At both spatial scales, Bradley (2002) showed no significant differences in nest success at sites adjacent to or far from forest edges. We conclude that the analysis by Zharikov et al. (2006) does not contribute to understanding murrelets' responses to edges or the effects of edges on nesting success.

Faulty use and interpretation of fragmentation and patch size data

There is clearly a problem in the way that Zharikov et al. (2006) defined and mapped patches of old forest. DS has experienced a much longer period of clearcut logging and, according to this paper, has lost 80% of the original forest cover, whereas CS has experienced relatively little logging and lost only about 25% of the forest cover. Zharikov et al. (2006) describe CS as "intact" and "much less fragmented" relative to DS. Having worked on marbled murrelet forest habitats in both areas, we believe that this interpretation is likely correct. However, a perusal of the actual forest patch data used by Zharikov et al. (2006) shows the opposite trend (Table 1): within the Minimum Convex Polygons established around the nest sites and used for the patch analysis, the density of forest patches is actually 1.5 times higher in CS than DS.

We were not able to resolve this apparent discrepancy with the data provided by Zharikov et al. (2006). Both of us have worked extensively in British Columbia with forest cover mapping used for industrial timber management and the Baseline Thematic Mapping system (http://ilmbwww.gov.bc.ca/cis/initiatives/ias/btm/index.html) and we are aware that many divisions into forest polygons are based on differences in dominant tree species composition or tree basal areas, and do not reflect actual patch boundaries as intended in this analysis. Furthermore, by setting boundaries on all streams, apparently without reference to their size, Zharikov et al. (2006) have created a far more patchy landscape than we believe would be perceived by a marbled

Table 1 Comparison of the number of forest patches within the Minimum Convex Polygons used for analysis in Desolation Sounds (DS) and Clayoquot Sounds (CS). Contrary to what is stated in the text by Zharikov et al. (2006), their data indicate proportionately greater patchiness in CS. This is most likely due to errors in delineating forest patches from mapped polygons

Parameter	DS	CS
Minimum Convex Polygon (ha)*	333,000	152,000
No. of forest patches*	10,154	6868
No. of patches per 1000 ha	30.5	45.2

* Zharikov et al. (2006: p. 111)

murrelet. We conclude that the patch area analysis performed by Zharikov et al. (2006) is therefore meaningless and the weak trends resulting from their analysis should be ignored.

Overemphasis of statistically significant but biologically trivial results

In their analysis of patch size use by nesting marbled murrelets, Zharikov et al. (2006) concluded that in DS there was disproportionate use of patches of ca. 10 ha and ca. 200 ha. No preferences for patch size were evident in CS. Ignoring the apparent preference for 200 ha patches in DS, their abstract states that murrelets "tended to nest in disproportionately smaller fragments" in this "logged" landscape. Even this interpretation of the data is open to question. If one examines their Figure 3 it is clear that there is no consistent trend towards smaller patches in DS (i.e., in the patches <210 ha), but only a difference within the 10 ha bin. Such a result could be an artifact of sampling, especially since the sample of nest sites (121) was much smaller than that of random (1000) points; the smaller sample of nests is more likely to contain irregularities in the histograms, relative to the smoother distribution of the larger random sample.

Given the doubts about the spatial resolution of these data and the way in which patches were defined (see above), it seems doubtful that this blip at ~10 ha represents a true selection. Indeed if one pools all the DS data for patches <210 ha, then about 70% of both nests and random points fall into this size class (percentages based on our reading of the columns in Figure 3 of Zharikov et al. 2006). In other words, murrelets used the patches in proportion to their availability (as found by Ripple et al. 2003) and there was no preference for small patches. We conclude that there is no support for the stated disproportionate use of small patches.

Zharikov et al. (2006) identified variables that contributed to statistically significant models and then compared these variables for nest and random sites (their Table 2) and for active and failed nests (their Table 4). If one compares the actual mean values given in the tables, relative to their variance (SD) and take into account the true spatial resolution of the data, it becomes obvious that nearly all the differences are trivial and would not stand up to rigorous univariate analysis (which is the way these variables are treated in the abstract and discussion). Even the strongly touted differences in distance to hard-edge clearcuts in DS represent differences of 0.46 km (relative to SDs of 1.35 and 1.46 km for nests and random points, respectively). In CS the differences between nests and random points for this measure were 0.30 km (compared with SDs of 1.68 and 1.74 km, respectively). The differences in slope, also strongly promoted, amount to 3^{o} in DS and 4^{o} in CS; these differences are probably smaller than the realistic resolution of the actual slope data and certainly smaller than the slope effects that can be applied in forest management.

Without detailed consideration of the size of the glaciers, prevailing winds and topography we cannot accept that glaciers that are on average 6.5 km from nest sites have the types of cooling effects mentioned by Zharikov et al. (2006). The two papers they cite in this regard deal with very different situations: sites within 500 m of a glacial front (Mizuno 1998) or at 1000 m elevation in British Columbia (Parish and Antos 2004). Similarly, we doubt that a difference of 0.91 km in the distance from glaciers between nests (6.51 km from glaciers) and random points (5.60 km) is biologically important when the mean distances from glaciers of both exceed 5 km. Aspect and exposure to winds (variables not considered by Zharikov et al. 2006) would have far greater effects on nest microclimates than the effects of distant glaciers.

A similar problem exists with their interpretations of distance to ocean in CS. We question whether a 3 km difference between nests and random points is biologically meaningful when the SD in each is >8 km, and murrelets are known to commute much greater distances (up to 100 km) between nest sites and marine foraging grounds (Whitworth et al. 2000; Hull et al. 2001). Estimated distances from the mouths of watersheds in CS to the nearest known foraging locations ranged from 1 to 28 km (Burger 2001: Appendix) and these distances should be added to the inland commuting flights made to nest sites in this area. It is more likely that murrelets would exhibit non-linear responses to the distance from the sea (Bahn and Newsom 2002), avoiding unfavourable shoreline habitats with high predator densities (Burger et al. 2000; Rodway and Regehr

2002) and also extreme commuting distances (perhaps those >30 km inland; Hull et al. 2001). Such quadradic-like trends might be difficult to model with logistic regression.

We believe that Zharikov et al. (2006) failed to provide convincing evidence of biologically significant differences between nest and random sites or between active and failed nests for any of the variables shown in their Tables 2 and 4. Given that these univariate differences were the foundation for their discussion and the conclusions in their abstract, we urge caution in accepting and applying their interpretations.

Ignoring uncertainties and biases in the methods, data and modeling approach

Zharikov et al. (2006) aim to remove the uncertainties associated with previously used audio-visual censuses (and incorrectly cite Burger 2001 which did not use this method). They fail, however, to adequately discuss the uncertainties and potential biases in their own data and methods. Foremost is the strong focus on analysis done in DS, where 80% of the original forest has been clearcut over the past 150 years. This logging was concentrated on the valley bottoms leaving commercially low-value forests (i.e., small trees unlikely to provide nesting habitat for murrelets) in low elevations and more accessible (i.e., less steep) slopes. This is almost certain to bias the habitat use of marbled murrelets nesting in the remnant forests. Bradley and Cooke (2001), who are co-authors in the Zharikov et al. paper, recognized this problem when discussing the use of unusual nest sites in DS on cliffs and a deciduous tree, and stated (p. 56): "The selection of these unusual nesting habitats by marbled murrelets may be due to heavy modifications of the original old-growth forest". Should the same not be true for many of the other nests found in DS? Do the results from CS, with relatively little forest loss, not represent a truer reflection on the habitat preferences of nesting murrelets? Zharikov et al. (2006) emphasize the results from DS throughout the paper, especially in the abstract and discussion, but we believe that the results from CS (that often produced contrary trends to DS) form a somewhat stronger basis for understanding habitat needs of the murrelet in British Columbia.

Caughley (1994) cautioned against analysing habitat preferences in severely depleted habitats, stating that we cannot assume that the remnants of once widespread and common species have settled on the most favoured habitat. The remnant populations are most likely to end up in the habitat least favourable to the agent of decline (in this case timber companies). As emphasized by Zharikov et al. (2006), murrelets and timber companies share preferences for the same type of forests, suggesting that the murrelets in DS are now nesting in less favorable habitat than was once available there.

As pointed out by Zharikov et al. (2006) nest success (survival of chick to 20 days) was similar in DS and CS, although the CS sample was small (29 nests). Superficially this might suggest that the higher fragmentation in DS has a negligible effect. But to prove this point, one should take into account the many variables that might affect breeding success in these widely separated study areas, including prey availability, competition for prey with other marine predators, and predator densities in the forests.

Zharikov et al. (2006; p. 116) mention that a significant proportion of the DS nests (about one quarter) were found in polygons that were not classified as old seral forest but as young or secondary forest or regenerating burned areas. The nests were therefore likely to be in small pockets of old-growth trees within otherwise unsuitable habitat. Zharikov et al. (2006) interpret this as proof that their results under-represent the usage of small patches. This might be true, but in order to prove this they should have considered such small pockets of old-growth within the random sample too. This was not possible with the forest cover data they used, but is possible with detailed air photo interpretation (Donaldson 2004). They need to show that these small pockets were used more frequently than expected by their availability. Until such analyses are completed, ideally in a less modified habitat than DS, the stated preferences for small patches remain speculative and unproven. Their inability to use a quarter of the DS nests in their analysis is further evidence of the serious problem of using coarse-scale satellite and forest cover data to test for finer-scaled biological processes like patch use and edge-effects.

Consistency with general understanding and other studies is an important criterion for validating modeling results. There is extensive literature on nesting habitat use by marbled murrelets (reviewed by Ralph et al. 1995; Nelson 1997; Burger 2002; McShane et al. 2004), but Zharikov et al. (2006) did not cite some relevant studies from British Columbia and elsewhere that reported contradictory evidence. For example, Rodway and Regehr (2002) reported significant negative effects of fragmentation on relative abundance of murrelets in CS. They also showed that canopy closure was higher near streams; therefore the effects of easier access to nest sites would be restricted to the trees immediately bordering streams only and not detectable at the spatial scales used by Zharikov et al. Other murrelet data that could have been more thoroughly discussed include: both positive and negative effects of steep slopes on murrelet occurrence (Burger 2002); negative edge effects on nest survival (Nelson and Hamer 1995; Manley and Nelson 1999); and negative effects on populations associated with forest fragmentation at larger spatial scales (Meyer and Miller 2002; Meyer et al. 2002; Raphael et al. 2002). We recognize that a paper of this nature need not cite all the pertinent literature, but the scarcity of discussion on contradictory evidence is troubling.

Conclusions

Given the problems with spatial resolution, models with low predictability, contradictory results and errors in interpretation identified above, we find little or no support for the major statements and conclusions made by Zharikov et al. (2006). Because of the high risks to marbled murrelets in implementing these findings, we strongly urge that application of the results of this paper in management of nesting habitat be done with great caution and with reference to the many contradictory studies. Managers also need to pay attention to the actual data presented in the paper and not just the interpreted conclusions. For example, if managers want to follow this paper and create more habitat where murrelets are forced to nest in close proximity to hard clear-cut edges, then a perusal of this paper suggests that “proximity” to edges implies a mean distance of 1.72 km (Zharikov et al. 2006, Table 4), and therefore a mean patch of at least 929 ha.

It is clear that the effects of patch size and forest edges on nesting marbled murrelets are complex, perhaps site-specific, and poorly understood. McShane et al. (2004) reached a similar conclusion based on an extensive review of available data. The Zharikov et al. (2006) analysis indicates that coarse-scale landscape-level analyses might not reveal biologically meaningful conclusions on patch and edge effects for murrelets. Studies using finer-scaled measures (resolution ~10 m) are needed. Furthermore, we conclude that analysis of edges and other fine-scaled habitat variables needs to include a much wider range of habitat variables, accurately reflecting the spatial scales at which murrelets are likely to make their choice of nest platform. Failures to consider appropriate parameters and spatial resolution can lead to misclassifications in habitat models (Huston 2002; O’Connor 2002; Beissinger et al. 2006). The low predictability of the models of Zharikov et al. (2006) indicates that many other variables not considered (e.g., tree size, moss development, canopy micro-structure, aspect, topographic complexity within stands) are likely to be more important habitat determinants for nesting murrelets than the coarse-scale variables used in this analysis.

Habitat models are frequently developed to deal with specific management or conservation issues. Unfortunately, managers making the field decisions might not have the time nor the experience to delve deeply into the data, results and interpretation of habitat models. Consequently they rely heavily on the interpretative text provided by the models’ authors, especially that given in the abstract and discussion (Beissinger et al. 2006). As we have pointed out, there can be errors or misinterpretations in models that are selected primarily on their statistical strengths. As multi-modeling and information-theoretic approaches become the dominant paradigm in ecology, authors, editors and reviewers of modeling papers have an important duty to put greater emphasis on the biological validity and realism of the models’ design, output and interpretation (O’Connor 2002; Beissinger et al. 2006).

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