THESIS

A METHOD TO QUANTIFY AND DEPICT UNCERTAINTY IN WILDLIFE HABITAT SUITABILITY MODELS USING BAYESIAN INFERENCE AND EXPERT OPINION

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY LEE E. O'BRIEN ENTITLED *A METHOD TO QUANTIFY AND DEPICT UNCERTAINTY IN WILDLIFE HABITAT SUITABILITY MODELS USING BAYESIAN INFERENCE AND EXPERT OPINION* BE ACCEPTED AS FULFILLING IN PART THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

A METHOD TO QUANTIFY AND DEPICT UNCERTAINTY
IN WILDLIFE HABITAT SUITABILITY MODELS
USING BAYESIAN INFERENCE AND EXPERT OPINION

Knowing the distribution of wildlife habitats across the landscape is an important component in biological conservation planning. Many conservation planning projects use wildlife habitat suitability models as the basis for predicting the distribution of habitat for terrestrial species. The predictions are typically binary GIS maps depicting the distribution of suitable versus unsuitable habitat, without indication of how strong the evidence is for these predictions across the area. There are many sources of uncertainty in these models as each data layer, with its own level of uncertainty, is incorporated into the models. Habitat suitability models are often knowledge-based and do not quantify their inherent uncertainty. Or, if the models are empirically-based, there are usually insufficient data to derive habitat distribution predictions and to test the predictions to determine the level of uncertainty associated with them. To make evident the uncertainty inherent in knowledge-based habitat suitability models, Bayesian inference procedures were used to combine expert opinions about the strength of wildlife habitat relationships with prior model parameters to create probability maps that depict the state of knowledge about the distribution of suitable habitat for terrestrial wildlife species. The Bayesian method has several advantages. One is that probability in a Bayesian framework is a direct representation of uncertainty. Thus models produced using this method are easy to understand and interpret. This method can be used on any species, regardless of the amount of empirical data available. Modeling species with deficient habitat relationship data produces appropriate results showing high levels of uncertainty. Bayesian methods allow the combination of empirical and knowledge-based evidence, so that all sources of information about species habitat may be incorporated. Bayesian models may also be updated, so that models can be improved as new information arises. The models can also incorporate landscape context and depict the associated uncertainty. With binary models, a priori decisions are made to include or reject specific habitat conditions. This tends to either over or under predict suitable habitat by including or rejecting borderline conditions. The portrayal of the results (habitat is suitable: yes or no) also implies a certainty that is unwarranted. With the Bayesian method, all possible habitat conditions are retained in the models, revealing areas of potentially suitable habitat that may have been omitted by binary models, and the certainty of the predictions is forthrightly depicted. The models derived by this method produce simple, honest, spatial depictions of what is known about the distribution of suitable wildlife habitat that can be used to support more informed decisions in species conservation planning and management.

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What a long strange trip it's been.
- Jerry Garcia

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INTRODUCTION

With the Rooseveltian era, however, came the Crusader for conservation... He insisted that our conquest of nature carried with it a moral responsibility for the perpetuation of the threatened forms of wild life. This avowal was a forward step of inestimable importance. In fact, to any one for whom wild things are something more than a pleasant diversion, it constitutes one of the milestones in moral evolution.

– Aldo Leopold 1933

Wildlife Habitat Suitability Models

Determining the configuration and distribution of suitable habitat for wildlife species has long been a goal of wildlife managers and conservation planners (Leopold 1933; Marmelstein 1978; Cooperrider et al. 1986; Verner et al. 1986; Morrison et al. 1998). Distribution of suitable habitat is usually mapped, either by direct observation of species occurrences (range maps) or modeled using relationships of species to specific habitat elements. Modeling is used in wildlife management to "define or reduce risk associated with complex decisions when data are scarce" (Roloff et al. 2001).

There are three primary ways that wildlife habitat relationships have been derived. Species occurrences have been used to determine if species occur with certain habitat elements out of proportion to the availability of those elements in a selected landscape (e.g., Chi-square tests). Wildlife habitat relationships can be derived by observing species distributions that tend to coincide with the distribution of certain habitat elements (e.g., multivariate statistical models, regression analysis, correlation analysis). Alternatively, habitat relationships can be postulated by species experts who have observed and learned the habitat use of species (e.g., knowledge-based models). Suitable habitat is spatially modeled for a species by locating the simultaneous occurrence of associated habitat elements across the landscape. Limiting factors such as minimum patch size, competition, barriers to movement, etc. can also be considered in models to create a more realistic representation of suitable habitat.

Wildlife species can live in an area only if basic resources such as food, water, and cover are present and they are adapted to the climatic extremes, competitors and predators in the area (Morrison et al. 1998). This area where a species can live is considered suitable habitat for that species. This concept differs from Elton's (1927) definition of a niche, the functional role and position of the organism in its community, in that habitat is only the geographic place having the necessary elements (resources) to provide for some portion of the life history needs of a species. There can be suitable habitat for breeding, feeding, resting, refugia, or migration. O'Conner (2002) describes habitat in the sense that it is used in this type of modeling as "...an envelope of environmental and vegetation requirements within which a species may occur." There is obviously a relationship between species occurrence and suitable habitat. Suitable habitat is defined as where a species can live, which is discerned in some manner from where species has lived; however, habitat does not necessarily need to be occupied to be considered suitable. Species may be absent from a particular habitat for reasons other than the suitability of the habitat resources (e.g. seasonal migration, exclusionary competition, disease, sustained control or harvest, local extirpation, etc.). There are also other factors that determine species presence, distribution and abundance such as predation, competition and disease, but those factors will not be considered here. This study focuses on distribution of suitable habitat and does not attempt to model species occurrence.

There are problems with using species occurrences to directly determine habitat suitability. One of the problems is that even if a species is found in a certain habitat type, it does not necessarily follow that the habitat is therefore suitable for sustaining the species. Species may occur in unsuitable (sink) habitats because suitable (source) habitats are saturated. The species' population would not persist without the presence of the source habitat (Van Horne 1983; Pulliam 1988).

Another problem in attempting to use occurrence to determine habitat suitability is that without comprehensive presence/absence data across the area of consideration, an accurate determination of which habitats are occupied and which are not cannot be made (Stockwell and Peters 1999). Even if occurrence were a direct indication of habitat suitability, accurate determinations of species habitat affinities cannot be made without presence *and* absence data. This data is lacking for a majority of species (Lyon et al. 1987; Morrison et al. 1998; Lele and Das 2000).

Several factors account for this paucity of presence/absence data. Rigorous survey data are often difficult to obtain. Many species are difficult to survey and extensive effort is required to determine if an area is occupied or not (Wilson and O'Brien 1994; Boone and Krohn 2000; Heglund 2002). Or, a particular habitat may not be occupied at the time of a survey and habitat that is suitable and important to the species survival may be mischaracterized as not being so. Not all suitable habitat will be occupied at any particular point in time (Cooperrider 1986; Gilpin and Hanski 1991; Morrison et al. 1998). Morrison et al. (1998) maintain that habitats need to be conserved even if they seem unoccupied. They argue that monitoring wildlife use of habitats should proceed for more than one season or year, perhaps several. To do this for all species in all locations at a regional scale would not be feasible.

Also, survey data that includes only species presence is inadequate to determine habitat suitability. If species occurrences alone are used to build models with no absence data (that is, data of sufficient detection effort to say with confidence that the species is absent from an area), then suitable habitat cannot be confidently delineated from unsuitable habitat, because there are no data available to establish which habitats are unsuitable. Another problem with occurrence data is the potential inaccuracies of the species location data and the overlay of this data with potentially inaccurate habitat parameter maps (McKelvey and Noon 2001).

To avoid the problems of using species occurrence data to determine habitat suitability, the type of habitat models used in this study are knowledge-based models, wherein species habitat affinities are selected by species experts as being the important determinants of suitable habitat for particular species. Knowledge-based habitat suitability models based upon wildlife habitat relationships are the type of models used by the U. S. Geological Survey, National Gap Analysis Program (Burley 1988; Scott et al. 1993; Butterfield et al. 1994; Boone and Krohn 2000). The output of these models, predicted terrestrial vertebrate habitat distributions, are used for species conservation planning by the Gap Analysis Program (GAP) and in other planning programs (the US Forest Service Species Conservation Program, the US Park Service Inventory and Monitoring Program, The Nature Conservancy Ecoregional Assessments, etc). Users of these types of habitat models need to know the credibility of the predictions made by the models.

Spatial (extent and grain) and temporal scales of habitat models must also be considered. Extent is a measure of how wide an area to be included in a model. Grain is a measure of the resolution, or how detailed a model is. Wiens and Rotenberry (1981) found the response of birds (distribution and abundance) differed with different scales of spatial resolution. They theorized that at a “between-habitat” scale birds were responding to habitat configuration and at “within-habitat” scale their response was more strongly correlated to habitat floristics. Ideally, the scale of models should be consistent with the scale relevant to the organism's point of view (Morrison et al. 1998; Wiens 2001; Heglund 2002). This is not always possible, because the conditions of relevant habitat elements may not be available at the appropriate scale. When the scale of a model differs from the scale relevant to the species, it should be disclosed along with the assumptions made during the modeling procedure, as well as considered in the goals and proper uses of the models.

For this study, habitat is modeled at a regional spatial scale; that is, a coarse grain and a large regional extent. This approach gives a regional overview of species habitat requirements, suitable for managing large tracts of land. This approach, however, may miss important fine-grained, "micro-habitat" conditions that are important to certain species. These elements (e.g., standing dead trees of a particular diameter) may not be directly modeled; instead surrogate habitat elements at a scale that can be modeled are used, with the assumption that larger scale elements will include finer scale elements (e.g., forest stands of an appropriate type and age will contain standing dead trees). The hope is that with conservation of large representative habitat types, that sufficient micro-habitat types will also be conserved (Margules and Usher 1981, Margules et al. 1988). This cannot be assumed without explicitly testing this relationship (Wiens 2002), so this becomes one of the assumptions of modeling at this scale.

Habitat condition and the distribution of habitat are not static. They change over time and the processes that produce habitat patterns operate at different scales (Wiens 1986). Habitat suitability models, based upon species associations with certain habitat elements and the co-occurrence of those elements, will accurately portray potentially suitable habitat whenever those elements co-occur, assuming the species habitat associations are correct. The models will not predict habitat suitability over time but, as element conditions and distributions are updated, the models will accurately predict suitable habitat under current conditions. The models capture a snapshot in time of a continually changing landscape.

Species populations and distributions also change over time (Cooperrider 1986; Gilpin and Hanski 1991). However, since these habitat suitability models are not modeling species occurrence, it is not imperative that they track changes in species distributions. Habitat can be suitable even without the species present.

It is increasingly apparent that considering only homogeneous habitat patches is not sufficient for understanding the habitat needs of taxa. Landscape metrics, such as patch context, boundary dynamics and connectivity of the landscape are essential considerations in describing suitable habitat for a species (Rolstad 1999; Wiens et al. 2002). Taking into account these landscape metrics changes the focus of habitat suitability models from delineating individual patches of suitable habitat to modeling functional landscapes from the taxa's point of view. Modeling functional landscapes (Flather et al. 2002; Theobald and Hobbs 2002) requires additional data, which add to the overall complexity and uncertainty in the models. The method presented here can be used to incorporate these landscape metrics and the additional uncertainty.

This study focuses on the habitat of terrestrial vertebrate species and does not consider other taxa, such as invertebrates (Ponder and Lunney 1999), fresh water species (Dodds 2002) or marine species (Norse 2001). Habitat modeling for these other taxa are beyond the scope of the study. The modeling procedures presented here, however, can theoretically be used at any scale and for any species, if there is a sufficient expert knowledge to derive them.

Uncertainty in Models

Whereas scientists are familiar with uncertainty and complexity, the public and policy makers often seek certainty and deterministic solutions... environmental policy is most effective if scientific uncertainty is incorporated into rigorous decision-theoretic framework as knowledge, not ignorance.

– Bradshaw and Borchers 2000

There is uncertainty in determining what habitat elements are important to a species. There is also uncertainty in spatial GIS models introduced by inaccuracies in landcover classifications (Flather et al. 1997), digital elevation models (Theobald 1989), species inventories (Flather and King 1992), and scale inconsistencies (Fotheringham 1989, Wiens 2001). Uncertainty inherent in spatial data layers is aggregated as the layers are overlaid in a GIS model (Openshaw 1989; Forier and Canters 1996; Heuvelink 1998). Veregin (1989) postulated that map accuracy declines exponentially with increasing number of data layers. Attempts to overlay individual habitat models to predict distribution of habitat richness can aggregate undetermined levels of uncertainty to potentially unacceptable amounts of error (Conroy and Noon 1996; Dean et al. 1997; Flather et al. 1997). Krohn (1996) argues that this is not a significant problem with the kind of models used in Gap Analysis because of the redundant nature of the information in different data layers. It is possible that the redundancy (or co-variation) of data layers may effect the relative values of the probabilities derived via this proposed method, whereas they did not seem to effect binary models (Krohn 1996). This must be disclosed when presenting these types of models.

This study will not deal with the various inaccuracies of the spatial data layers used in the habitat models, except that a method will be proposed to incorporate inaccuracies in the landcover classification, likely the largest source of error. The focus of the study is the uncertainty associated with wildlife habitat relationships and how to incorporate and spatially depict that uncertainty. Uncertainty in the spatial layers of the model are left to be dealt with by the creators of those datasets. If uncertainty in these layers is quantified, it can be incorporated into the habitat models using this proposed method.

Much of the uncertainty in ecological models is inevitable because of practical as well as theoretical limitations. For spatial models such as these, with transient and often difficult to detect subjects, it is often impossible to compare them to independent measures of “truth” (Stoms et al. 1992). So, to be credible, the models must honestly reflect the accumulated uncertainty that is inherent in their development (Flather et al. 1997).

Acknowledging the need for explicit depiction of uncertainty associated with models is not new. Fedra et al. (1981) argued that model-based predictions should at least reveal their dependence on and sensitivity to uncertainty and assumptions. Cooperrider (1986) wrote: “Since models produce predictions rather than absolute truths, uncertainty is always associated with their predictions; use of models that predict occurrence *probability* are more realistic because they attempt to quantify the uncertainty associated with the predictions.” Bradshaw and Borchers (2000) argue that it is imperative to effectively articulate the uncertainty in scientific predictions to policy makers so that adaptable, resilient policy decisions can be made. Block et al. (1994) went so far as to recommend that wildlife habitat relationship models *not* be used by land managers who do not possess the expertise to evaluate the accuracy of the models’ output.

In the context of using spatial GIS models in risk assessment, Rejeski (1993) lists four issues that must be addressed in establishing scientific credibility:

1) Believability – are the models and supporting data properly chosen?

2) Honesty – have uncertainties inherent in the analysis been conveyed?

3) Decision Utility – does the analysis provide a clear basis for action?

4) Clarity – are the maps understandable and sensitive to perceptual differences of the intended audience?

Since the goal of creating habitat suitability models is to provide planners, managers and the public with credible information on which to make informed decisions on land management issues, the models should meet these criteria. The goal of this study is to fulfill each of these requirements for credibility by developing a method that explicitly incorporates uncertainty into habitat suitability modeling.

Depicting the uncertainty associated with data is important for users of the models to understand the strengths and limits of the models and get the "state-of-knowledge" about species habitat distribution. "Knowledge about uncertainty is important for effective use of ecological map displays and overlays. It impacts upon reliability and credibility of data representation, decision making, and model building" (Buttenfield 2001).

Most attempts to validate habitat models have been done by using occurrence data not used to create the model and comparing these to the model predictions, noting errors of omission and commission. (Avery and Van Riper III 1990; Block et al. 1994; Garrison and Lupo 2002; Karl et al. 2002). Errors of commission (also known as Type I errors) are said to have occurred when an area predicted to be habitat for a species is not found to have any occurrence records associated with it. Errors of omission (also known as Type II errors) are said to have occurred when an area that is not predicted to be habitat for a species has occurrence records for the species. If independent occurrence data are not available, resampling the data that went into building the models and using those for validation has been recommended (Verbyla and Litvaitis 1989, Guisan and Zimmermann 2000).

To add credibility to the type of knowledge-based habitat models used by GAP, Csuti and Crist (1998) recommended that the models be "validated" by comparing the predicted habitat distributions with species occurrence data. The recommendation has been to use species occurrence lists from parks or forest units and overlay these areas with the habitat suitability maps and look for errors of omission and commission (Edwards et al. 1996). This procedure is also called "measures of agreement" to distinguish it from true model validation (Csuti and Crist 1998). However, for the same reasons that species occurrences should not be used to determine habitat suitability, they should also not be used to test the validity of habitat suitability models.

There are several problems with attempting to validate habitat models with occurrence data. Spatial and temporal scale issues affect the associations of species with habitat (Wiens 2001). The spatial scale (resolution) at which the model is predicting habitat may differ from the scale of the geographical unit used to test it (Flather and King 1992). Is it known which habitat patches within a park or forest unit the species occupies, or is it only known that the species occurs somewhere in the unit? If predicted suitable habitat for a species overlaps one small corner of a unit, and the species in question occurs in a different habitat type in the unit, will that be considered verification of the model?

If a species is known to occur in an area that the model failed to predict as suitable habitat (an error of omission), the model may be in error, or a species may be located in "sink" habitat types that will not sustain it because it was forced out of suitable habitat types (Van Horne 1983; Pulliam 1988), or the species may be wandering between suitable habitat types (Morrison et al. 1998). If, however, there are no records of a species occurring in an area that the model predicts as suitable habitat, or if a survey is done and the species is not found in an area that the model predicts is suitable habitat (errors of commission), these are not necessarily indications that the model is wrong (Dedon et al. 1986; Avery and Van Riper 1990; Block et al. 1994; Karl et al. 2002). The species may be absent because of seasonal migration, competitive pressure, control or harvesting, or they may be temporarily extinct in that particular habitat patch (extirpated), or the survey may have missed the species' occurrence due to inadequate sampling, and the habitat may actually be quite suitable and important to the species, as defined previously.

Since presently unoccupied habitat is not necessarily unsuitable habitat, and since these models are predicting the distribution of suitable habitat and not species occurrence, using species occurrence to validate habitat suitability models is not a relevant test of their validity. This study will present a method to indicate the uncertainty inherent in knowledge-based habitat suitability models by incorporating the uncertainty in the knowledge used to develop the models. The uncertainty will be spatially presented to show where the evidence is and is not strong. Mapping uncertainty allows users to identity patterns of dense or sparse data and evaluate the fitness of the data for particular applications (Buttenfield 2001). Spatially depicting uncertainty is also useful for bringing to attention areas that should receive further investigation (Miller et al. 2004).

Another method for adding credibility to models is to conduct sensitivity analysis, to test how sensitive predictions are to inaccuracies in input data (Stoms et al. 1992). The models presented here will be tested as to their sensitivity to prior probability inputs and erroneous conditional probabilities.

Bayesian Inference

The Bayesian method is a normative and rational approach for decision making and emulates the way in which a wildlife expert might be expected to make decisions over habitat suitability for a species.

– Aspinall and Veitch 1993

Bayesian inference is based on the idea that probability is orderly opinion and that inference is the revision of probabilities in light of new information. In the Bayesian framework, probability describes uncertainty (Luce and O'Hagan 2003). Bayes' theorem provides a formal method for decision making under conditions of uncertainty, providing a method to revise opinions (subjective probabilities) in light of new information (conditional probabilities) (Aspinall and Vietch 1993). The general Bayes' theorem is expressed by the following expression:

$$P(x|y) = \frac{P(x)*P(y|x)}{P(x)*P(y|x) + (1-P(x)*1-P(y|x))}$$

where:

P(x) = prior probability (probability of condition of interest; x)
P(y|x) = new information (probability of y for condition x)
P(x|y) = posterior probability (of x) given new information (y)

Bayesian inference relies on prior knowledge (prior probabilities). Often times there is no prior information about the question at hand, so prior probabilities are guessed at or "non-informative" prior probabilities are used. A non-informative prior is one that does not have inordinate influence on the outcome of the inference (Luce and O'Hagan 2003). In binary (yes or no, 1 or 0) questions, the non-informative prior is 0.5, halfway between 1 and 0 (yes and no). The degree of variation from 0.5 affects the magnitude of influence that the prior probability has on the final probability calculations (See Figure 1).

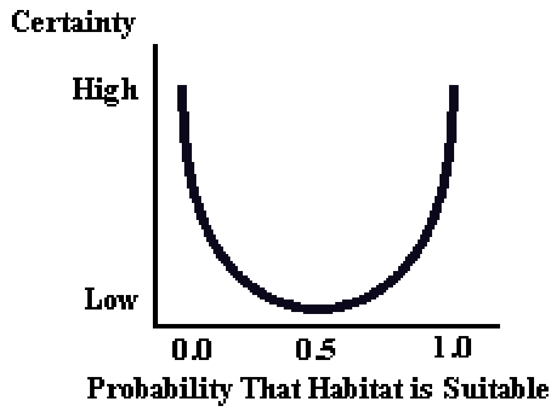


Figure 1. Probability as Measure of (Un)certainty.

It should be noted that what is being modeled in this study is a binary response; whether habitat is suitable, yes or no. Habitat quality is not modeled. The X axis in Figure 1 and posterior probability depictions are not gradients of habitat quality, rather they represent the probability of a particular habitat being suitable.

Bayesian methods lend themselves well to studies with incomplete data or studies where replication is not an option (Reckhow 1990). Bayesian methods handle these types of conditions, often encountered in ecological studies, better than traditional scientific methods and frequentist statistics (Hilborn and Ludwig 1993). Because Bayesian information is summarized as probabilities, the results of multiple experiments or data from different sources can be combined. Also, in a Bayesian framework probabilities are measures of uncertainty and can be used by decision makers as direct portrayals of the certainty of information (Dixon and Ellison 1996).

Decisions about the management of environmental resources are made without complete and certain knowledge, therefore they should reflect the inherent uncertainty, and they should be able to be modified when new information becomes available (Ellison 1996). Models based upon Bayesian methods fill both these needs, thus they are well suited as support for decision making. Ellison (1996) argues that Bayesian methods make better use of pre-existing data, allow stronger conclusions to be made from large-scale experiments with few replicates, and are more relevant to environmental decision making.

Bayesian inference has become prominent recently because of its extensive use in the medical profession, where decisions often have to be made with incomplete knowledge (Lusted 1968; Luce and O'Hagan 2003). Bayes' theorem provides a way to combine knowledge about symptoms into a framework for diagnosing disease.

Similar methods were adapted by geoscientists to predict the spatial distribution of mineral deposits (Bonham-Carter et al. 1988; Agterberg et al. 1990; Bonham-Carter et al. 1990; Katz 1991; Agterberg et al. 1993). This method is called weights-of-evidence. Weights-of-evidence requires location data of the parameter to be modeled and is only applicable in regions where the response variable is well known (Bonham-Carter 1994). This method has been used in some biotic models. Mensing et al. (2000) used a weights-of-evidence procedure to predict the location of packrat middens. This method can be used in situations where there is comprehensive presence/absence data.

Williams et al. (1977) adapted the Bayesian methods used in the medical profession to predict whether particular habitat sites could support certain densities of wildlife species. This method, known as pattern recognition (PATREC), used an estimated degree of association between habitat attributes and species population density as conditional probabilities and used Bayes' theorem to predict the probability that a new site would support a certain population density, given the habitat conditions. The habitat association estimates were derived using the percentage of occupied habitats from species population surveys. Prior probabilities were guessed at, or the value of 0.5 ("50-50 chance") was used (Williams et al. 1977; Kling 1980; Grubb 1988). Flather (1982) noted shortfalls of the PATREC method, including not taking into account ecological interactions (e.g. competition, territoriality, carrying capacity, etc) that should be addressed when attempting to describe the distribution of species population densities. This method of attempting to predict potential population densities also has the same problems associated with using species occurrence to develop habitat associations.

Others have used Bayesian inference to predict the probability of species occurrences based on known locations. Tucker et al. (1997) used survey data to estimate probability of bird occurrences, given certain habitat elements (landcover from satellite imagery, elevation and slope). They encountered problems with incomplete survey data, satellite imagery limits in delineating habitat types, using a single prior probability for all areas (they recommend using a geographically weighted prior), spatial resolution of datasets, and inaccuracy of the datasets. Johnson (1989) used empirical Bayes estimators to increase the accuracy of estimates of duck population sizes. Hepinstall and Sader (1997) used survey data (breeding bird surveys) and satellite imagery with Bayesian statistics to predict probabilities of bird occurrences. Vitale et al. (2001) did they same thing with bird census points they collected. Aspinall (1992) used Bayesian inference with known locations to map the distribution of red deer in Scotland. Aspinall and Vietch (1993) used a similar technique to map the distribution of curlew, but without using a landcover classification. They instead overlaid curlew locations directly onto a satellite image and a digital elevation model (DEM), thereby skipping the potentially error producing steps of classifying landcover and developing species habitat relationships.

All of these examples of using Bayesian inference involved using survey data and predicting species occurrence or population sizes. Other uses of Bayesian statistics to answer natural resource questions include using census data to evaluate the survival of trees (Clark and Lavine 2001), using prior beliefs about the species occurrence to predict whether a species will be present at random sampling points where it has not been observed (Nicholson and Barry 1995), using Bayesian updating to estimate demographic parameters such as mortality rates of owl populations (Linacre et al. 2003), and using elicited information from remote sensing specialists to develop Bayesian estimates of landcover classification accuracy (Green and Strawderman 1994).

Wintle et al. (2003) used Bayesian averaging methods to combine logistic-regression habitat models. They compared the predictions of Bayesian averaged models and "best" models select by Akaike's information criteria (AIC) a model selection criteria to independent occurrence data and found that the Bayesian averaged models did as well as the best models, while incorporating uncertainty in the choice of model structure.

Use of Bayesian methods in ecological studies is increasing. Almost all of these methods use empirical data to modify prior subjective opinion. The method proposed here uses expert opinion to disclose the inherent uncertainty in existing knowledge-based habitat models. Bayesian inference was chosen for this application because there were existing habitat suitability models for the species of interest that represent the best knowledge to date (for prior probabilities); all relevant data (empirical and expert) can be included in the models; models can be updated when new information becomes available; and model results are easily interpretable and honestly reflect the state of knowledge (or lack of knowledge) about the distribution of suitable habitat.

Expert Opinion

In many cases, models are developed by using a group of species experts. Even though every function or assumption of the model is not backed up by extensive research, a model that represents an expert consensus is easy to defend.

– Cooperrider 1986

Because the types of habitat suitability models used in this study are knowledge-based (as opposed to empirically derived), it is important to evaluate the use of expert opinion in making inferences. The knowledge of experts has to be quantified in some way. With Boolean (yes or no, 1 or 0) questions, this is fairly straightforward. Does species "A" use habitat element "X" for part of its life history, yes or no? This is how knowledge-based models are traditionally developed, either by direct inquiry or by searching literature in which these relationships have been reported by experts. Eliciting a quantitative response from experts as to the certainty of their opinions is more difficult.

Some argue that because expert opinions are subjective, they are therefore unsuited to defensible scientific discovery (Dennis 1996). However, experts can have complex knowledge that may not be expressed in empirical data alone. Tonelli (1999) argued that "rather than the lowest form of empirical evidence, expert opinion could easily be viewed as the highest form of clinical experience and judgment...". Fisher (1989) stated that for areas with uncertainty the Boolean approach is inappropriate and that an expert, knowledge-based approach should be used to improve reliability.

There is a vast body of literature devoted to evaluating methods of eliciting opinions from experts, and expert opinion is used in many scientific disciplines (Hoffman 1987; Cleaves 1994; Tonelli 1999). For example, formal methods have been developed to extract knowledge from experts for artificial intelligence systems (Hoffman 1987).

Artificial intelligence systems use expert knowledge to provide decision support for a wide variety of uses (Robinson et al. 1987).

Expert opinion and Bayesian methods are used extensively in risk assessment and reliability modeling, because experiments on situations such as failing bridges or leaking nuclear waste cannot be conducted (Thorne 1993; Rosqvist 2000; Sigurdsson et al. 2001). Expert opinion is also frequently used in the field of medicine to develop systematic procedures to assist practitioners and patients in making decisions about appropriate health care (Kahn et al. 1997; Tonelli 1999).

Expert opinion has also been used in research and management of natural resources. Hill et al. (1997) mapped predicted distribution of fescue grasses through knowledge-based modeling of environmental conditions known to occur where the grasses grew. Lawrence et al. (1997) used expert opinion in a decision support system (DSS) to help guide decisions in managing rangelands. Holthausen et al. (1994) used expert opinion to evaluate habitat suitability models for elk and found close agreement between expert opinion and empirical/knowledge-based model predictions. Stockwell and Peters (1999) used expert opinion to evaluate their Genetic Algorithm for Rule-set Production (GARP) models, which predict species distribution based upon locations and habitat distributions.

Some studies have called the use of expert opinion into question. Pearce et al. (2001) used expert opinion to attempt to refine predictive maps of faunal distribution based upon remotely mapped vegetation and found that expert opinion-derived maps were not as good as maps derived from robust survey data in predicting species occurrence when compared against independent occurrence data. Clevenger et al. (2002) found that knowledge-based habitat models based upon literature review did better (as compared to an empirical model) than those based solely on expert opinion. They attribute this to the possibility that opinions expressed in the literature are based upon collected data that has been statistically analyzed and summarized. These conclusions are called into question, however, because of the problems mentioned earlier associated with using species occurrences to test habitat models.

This is not to say that empirical data, when sufficiently available, is not preferable to expert opinion for estimating environmental parameters. O'Hagan and Luce (2003) caution that elicited responses from experts should not be considered as precise estimators of parameters. Lele and Das (2000) considered elicited opinions from experts as "guess values" and used them along with empirical data (insufficient on its own) in a hierarchical structure in a Bayesian update to prior information. Kaplan (1992) proposed a method that distinguishes between eliciting "expert opinion" and eliciting "expert information". He argued that instead of asking an expert's opinion about a parameter, experts should be asked what experience and information they have that is relevant to the value of the parameter.

For this application, expert opinion is not being used to estimate a fixed parameter. Instead, this method quantifies the uncertainty an expert associates with a particular species habitat relationship. In knowledge-based models, species habitat relationships are observer-based conceptions that are attempts to see the world through the eyes of the species. The uncertainty inherent in these observed relationships are the uncertainties of the species expert defining the relationships. So, when a species expert claims that she is "95 percent certain that xeric upland shrub steppe constitutes a suitable habitat element for this particular species", then that elicited quantity is the exact measure of the (un)certainty.

Commonly, habitat relationships have been developed by plotting species occurrences on parameter maps and noting which values of the parameters coincide with the occurrences and then extrapolating to new areas with similar parameter values (Stockwell and Peters 1999). Problems with this method, mentioned earlier, include potential inaccuracy of the locations, the extent of sampling and non-reporting of absence data, sampled but unoccupied suitable habitat, occurrence not coinciding with truly suitable habitat, map scale, and deciding which parameter maps to use. Ultimately, someone familiar with the species habitat use must decide which parameters are to be measured (to determine which habitat parameters to include in the analysis). Species experts have a sense for what habitat parameters are important to a particular species through direct experience and research and they can relate how certain they are about this knowledge.

The method proposed in this study encourages experts to consult any data that is available and combines the opinions of all participating experts. If new experts review the results and disagree (or agree) with particular parameters in the model, their opinions can be incorporated into the model, so that over time the models reflect the current state of knowledge about predicted distribution of suitable habitat. In areas where experts agree, certainty will increase and in areas of disagreement, certainty will be reduced.

Empirical data in the form of species locations are also used in the modeling process, not to predict suitable habitat, but presented to species experts to support their elicitation of confidence in the geographic range of species. Species ranges are used as constraints on the geographic extent of the models.

STUDY DESIGN

The use of models is based upon the concept that models can synthesize the best understanding of the situation given current information... Assumptions and interactions need to be clearly set forth. Often, this kind of information is exactly what a resource manger needs to make decisions.

– Virginia H. Dale 2003

The impetus for this study was to address one of the long standing criticisms of wildlife habitat suitability models of the type used by GAP (Butterfield et al. 1994; Boone and Krohn 2000; Csuti and Crist 2000). Because these habitat models don't quantify the uncertainty in their predictions, users have no gauge of their credibility (Stoms et al. 1992; Edwards et al. 1996; Dean et al. 1997; Flather et al. 1997; McKelvey and Noon 2001). The proposal to validate these type of habitat models by using species locations to show "measures of agreement" between habitat suitability models and species habitat use (Csuti and Crist 1998) is inadequate. The models predict the distribution of suitable habitat across a landscape, not species occurrence, so species occurrence should not be used to evaluate them. Besides, comprehensive species occurrence data for most species is unavailable.

The goal of this of this study is to develop a method to quantify the uncertainty inherent in knowledge-based habitat suitability models and to spatially depict this uncertainty, so that users of the models can see the certainty of model predictions across the landscape. The ultimate goal of this work is to add credibility to these types of wildlife habitat suitability models. The specific objectives are to: 1) quantify and depict the uncertainty inherent in knowledge-based wildlife habitat suitability models, 2) evaluate the use of Bayesian methods to integrate different types of data (empirical and knowledge-based) into the models, 3) evaluate how the models handle the addition of different sources of uncertainty, multiple reviewers, and additional model parameters, and 4) evaluate the usefulness of this method of creating wildlife habitat suitability probability maps to conservation planners and managers.

The basic design of the modeling procedures followed Bayes' Theorem, where prior knowledge (prior probabilities) is updated with new knowledge (likelihood function) to produce new understanding (posterior probabilities). In this case, the prior knowledge came from prior habitat suitability models developed for the Colorado Gap Analysis Project (Schrupp et al. 2000) with the best data available at the time. These were converted into probability surfaces depicting spatially explicit prior probabilities.

The updates to these prior probabilities come from species experts reviewing the species habitat relationships used in the models and giving their opinions on the certainty of the relationships (and proposing new relationships if they thought they were warranted). The elicited responses are used to create probability surfaces of the certainty of the species habitat relations for each habitat parameter. The probability surfaces of each habitat parameter (landcover, elevation, and geographic ranges) were combined by averaging them together pixel by pixel. In averaging the habitat parameter probabilities, twice the weight was given to the landcover data than to elevation or geographic ranges. The reasoning for this was that landcover data is the major predictor of habitat distribution in these models, whereas elevation and geographic range are constraints on where habitat can be modeled. The product of averaging these datasets together is a probability surface representing the likelihood function used to update the prior probabilities.

The prior probability surface and the likelihood probability surface are then combined using Bayes' Theorem to produce a posterior probability surface, which, in a

Bayesian framework, represents uncertainty. Thus you have a spatial representation of the certainty of habitat suitability distribution predictions across the landscape.

Variations on this basic model include incorporating inaccuracies in the landcover classification as an additional source of uncertainty in the models, combining the opinions of multiple species experts in one model, and including landscape context (e.g., minimum patch size, connectivity, barriers to movement) in the models and reflecting the added uncertainty that these would bring to the models. The design of the study is depicted in the flowchart in Figure 2.

Three representative Colorado wildlife species were selected for case studies to test the basic model methodology and the additional variations sequentially. The species selected were species of "special concern" as listed by managing/planning agencies and species for which there were experts readily available for participation in the study. The species selected were the mountain plover (*Charadrius montanus*), used to test the basic model design; the boreal toad (*Bufo boreas*), used to test the inclusion of multiple species reviewers in a single model and the addition of a proximity to water habitat parameter; and the lynx (*Lynx canadensis*), used to test the inclusion of landscape configuration constraints on the habitat model. Also, a landcover fuzzy accuracy assessment was included in the model to illustrate how inclusion of uncertainty inherent in the base data layers can be incorporated and effect the overall uncertainty of the model predictions.

The assumptions made in developing these habitat suitability models are that modeling habitat at a large regional scale will encompass the micro-habitats required for the viability of the species, that the prior probabilities (prior model results) are acceptable representations of what is known about habitat suitability for the species under consideration, and that potential covariation between datasets will not substantially effect the model outputs.

This modeling method is evaluated by ascertaining how feasible it is to carry out and whether the models meet the criteria for credible information for decision makers as described by Rejeski (1993). The model results are also compared to the original binary models to ascertain the differences and sensitivity analyses are conducted to ascertain the sensitivity of the models to differentially weighting habitat parameters, prior probabilities, errant conditional probabilities, and the order that multiple expert opinions are entered into the Bayes' calculations in the iterative approach. The modeling procedure is not evaluated with species occurrence or abundance data due to the problems, mentioned earlier, associated with this kind of data and because the models are of suitable habitat, not species occurrence; rather the method is judged by how well it conveys what is known (the current state of knowledge) about the distribution of suitable habitat. This is not to imply that species occurrence is not an important metric in conservation planning. The suitable habitat distribution maps produced by this method could potentially be used as starting points in adaptive management or to test hypotheses about species presence/absence.

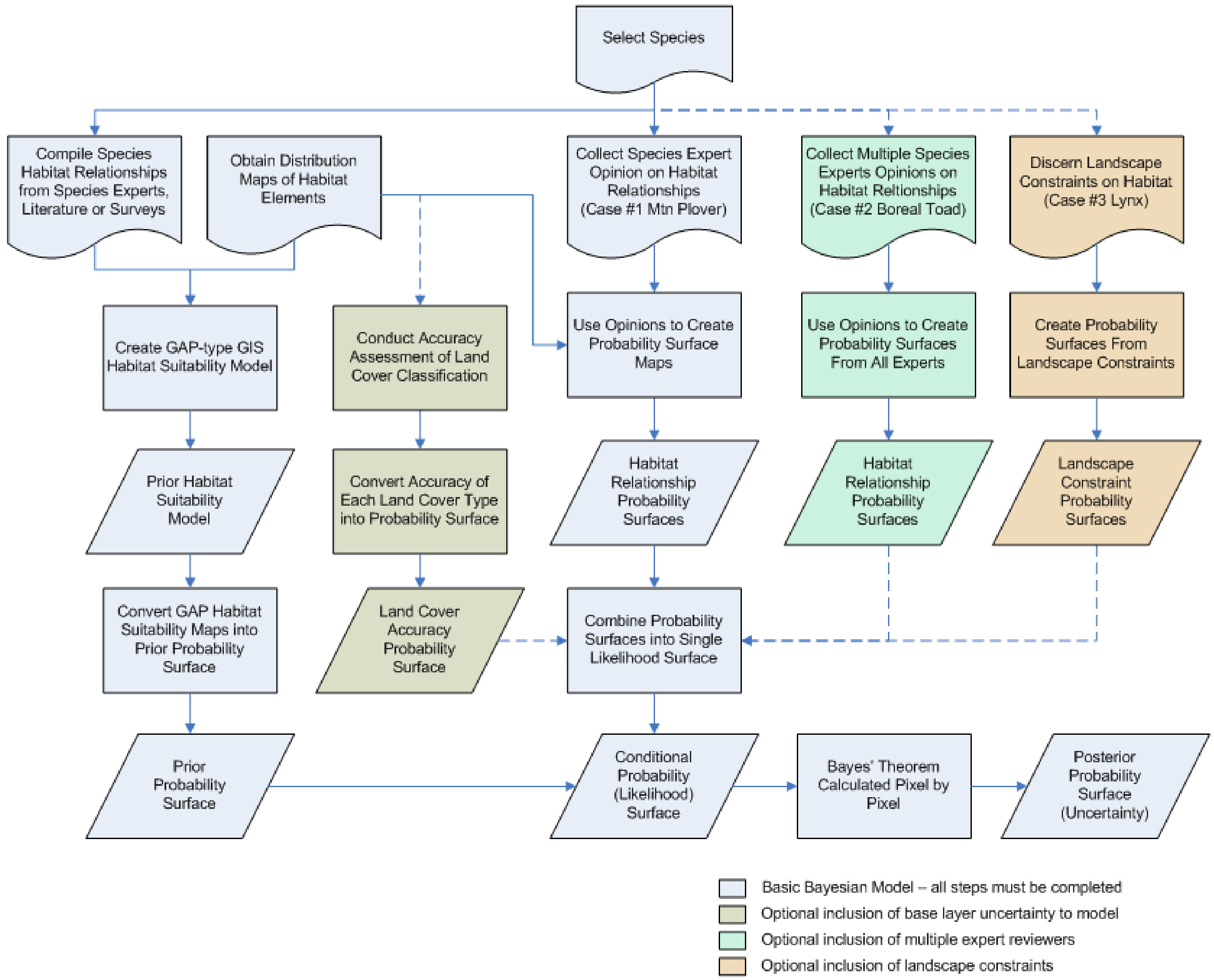


Figure 2. Flowchart of Study Design.

METHODS

Fortunately we already know a great deal about wildlife and their habitat relationships... It is imperative that we take this knowledge and interject ourselves into the mainstream of resource decision making with the most persuasive information that we can muster. And we must never forget that the time schedule is set by someone else. Land management decisions that affect wildlife resources ***will*** *continue to be made by someone; ...those decisions should be based on input from wildlife specialists using the best information available at the time.*

- F. Dale Robertson (in Verner et al. 1986)

Prior Probability Surfaces

Habitat models developed for Colorado GAP (Schrupp et al. 2000) were used as a starting point for applying the methods developed for this study. These habitat suitability models were developed using wildlife habitat relationship data obtained from taxon specific literature (Hammerson 1982; Andrews and Righter 1992; Fitzgerald et al. 1994; Kingery 1998), the Colorado Wildlife Species Database (Schrupp and Cade 1989), and other databases of species occurrences and species expert opinions. Range constraints were also derived from species location data and expert opinion.

Raster GIS maps with 30 m x 30 m cell sizes of landcover, elevation, streams, lakes and modeled riparian areas (Theobald et al. 1998) were developed and used with species affinities to determine “suitable” areas on each data layer. Using ESRI ArcView 3.3, a geographic information system (GIS), the data layers were overlaid (binary grids of 0's and 1's were multiplied together so that only areas that were suitable (1's) in all grids were retained) so that areas that met all habitat affinity conditions and were within range constraints were considered suitable habitat. Everything outside of this range was considered unsuitable habitat. This procedure was used to produce binary maps of the predicted distribution of suitable and unsuitable habitat for all Colorado terrestrial vertebrate species.

In addition, the predicted suitable habitat category of the Colorado GAP models was divided into “potential” and “likely” habitat. A region algorithm (RegionGroup) in ArcView was used to convert areas of contiguous pixels (in this case, all 8 pixels around a central pixel) of suitable habitat on the raster maps into individual habitat patches. These habitat patch maps were overlaid on maps of known or likely species occurrence for each county, which were developed from occurrence records and expert opinion. If a patch of suitable habitat intersected a county of known or likely species occurrence, the habitat patch was labeled “likely” habitat. Habitat patches that did not intersect counties of known or likely species occurrence were labeled “potential” habitat (Schrupp et al. 2000). This created three habitat categories: non, potential and likely habitat (Figure 3).

To be able to include these categories as prior probabilities in the Bayesian calculations of uncertainty, the categories had to be assigned probabilities of being suitable habitat. Since the probability in this study is associated with a binary variable (suitable or unsuitable habitat), probability values at the extremes reflect high certainty of either case. Low probability values (near 0) reflect high certainty of habitat being unsuitable, probability values near 0.5 reflect low certainty of anything, and high probability values (near 1) reflect high certainty of habitat being suitable (Figure 1).

The starting point for selecting prior probabilities was 0.5, the “non-informative” prior. In order not to over-predict suitable habitat in the final calculations, “likely habitat” in the previous models was assigned a 0.6 prior probability of being suitable habitat, “potential habitat” was assigned a 0.5 prior probability of being suitable habitat and “non-habitat” was assigned a 0.1 prior probability of being suitable habitat (Figure 4).

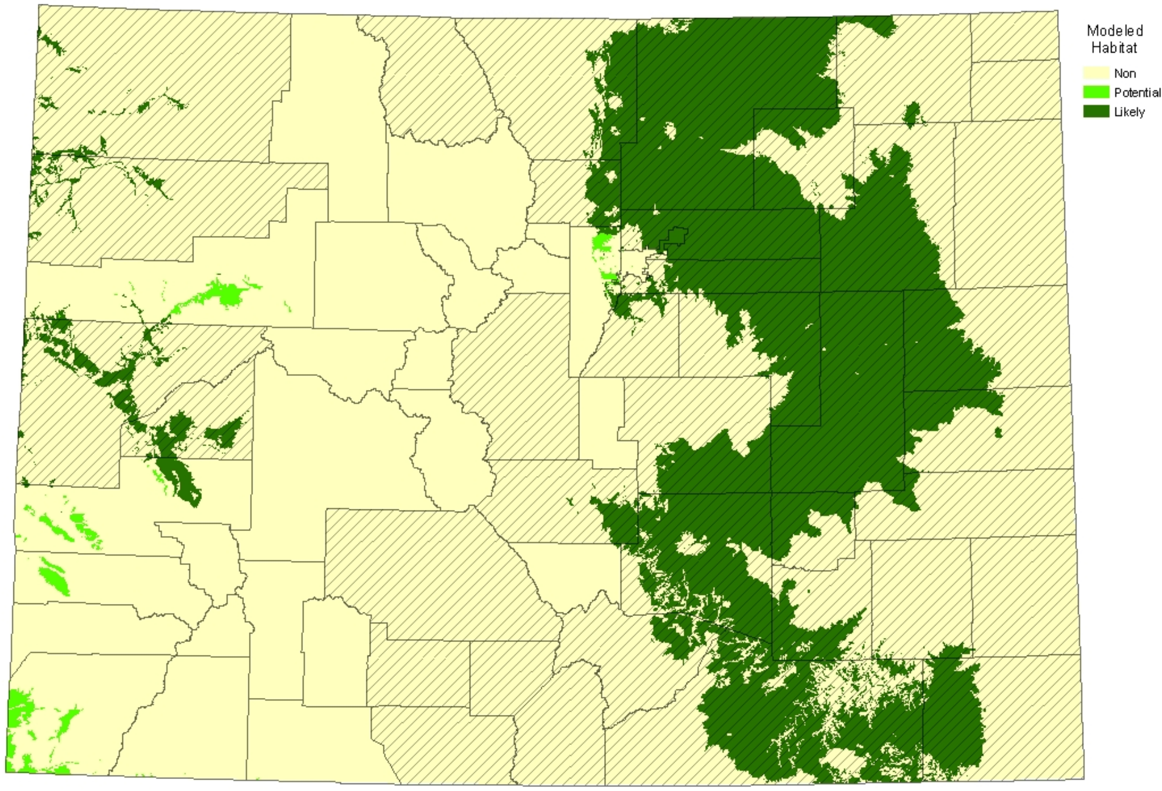


Figure 3. Prior Habitat Model. An example of a GIS habitat suitability model developed for the Colorado Gap Analysis Project. The model shows 3 categories of habitat for the mountain plover in Colorado (non, potential and likely habitat) and counties of "known or likely" species occurrence (hatched) and no known species occurrence (not hatched).

The influence of these assignments on the model are tested later in a sensitivity analysis. Each pixel in the raster dataset then was assigned a value of 0.1, 0.5 or 0.6. [Because ArcView grids with cell values of less than one ("floating point values") have limited functionality, probability values were multiplied by 1000 before being used in the raster grids. Using 1000 allowed the probabilities to have a precision of three decimal places. So, although the map legends show probability values from 0 to 1, the values stored in the grid cells are actually whole numbers from 0 to 1000.] These probability surfaces for the selected test species were used as the prior probabilities in the Bayesian inference calculations to ultimately reveal the uncertainty inherent in the models.

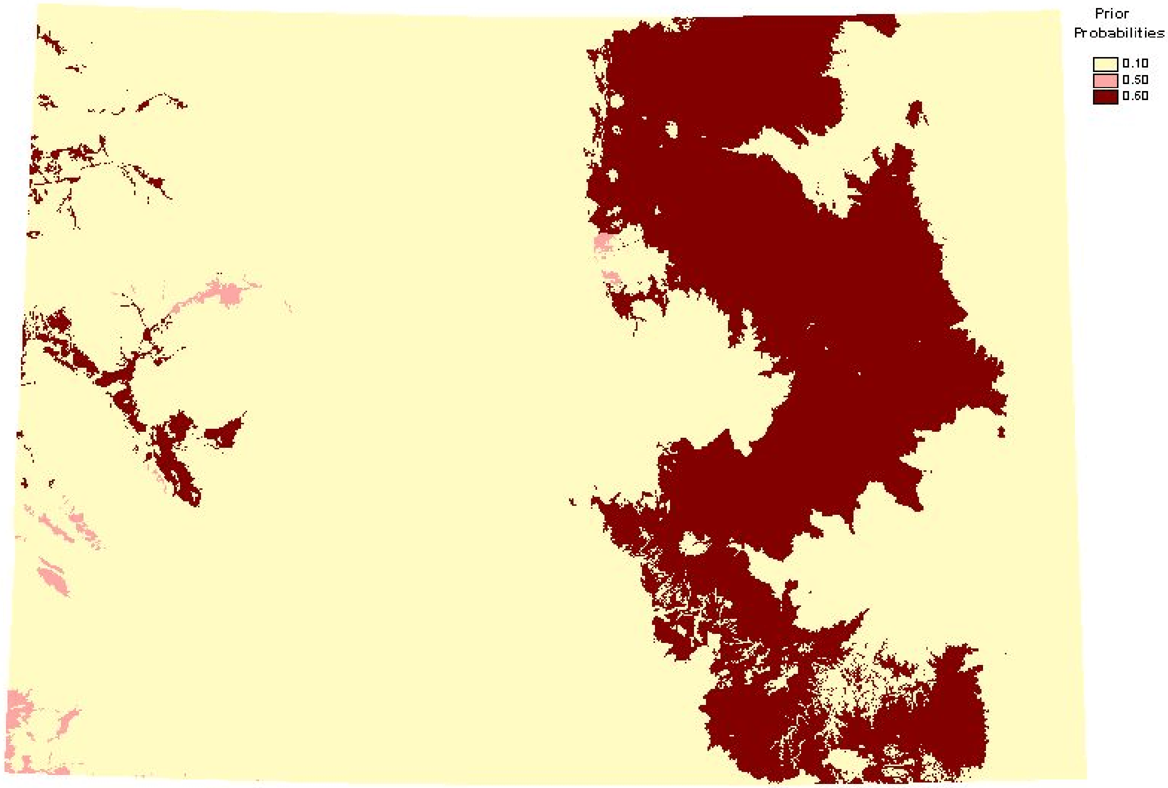


Figure 4. Prior Probability Surface. An example of assignment of habitat categories for the mountain plover of non, potential and likely habitat to 0.1, 0.5, and 0.6 respectively representing the prior probability of the habitat being suitable.

This procedure of assigning prior probabilities can be done with any habitat models prior to updating with opinions of species experts.

Quantifying Expert Opinions

The next step was to elicit opinions from species experts on each of the parameters (landcover, elevation, proximity to water, geographic range) that were used in the models for each species of interest. In order to be consistent and provide species experts with an easy means of reviewing the model parameters, a set of tools was developed for reviewing model parameters and collecting elicited expert opinions.

The first tool was developed to review the geographic ranges of species and collect expert opinion to update the range maps (O'Brien 2003). This tool was developed in ESRI ArcView GIS. The range data available for Colorado GAP (Schrupp et al. 2000) were species occurrence data and expert opinions about the ranges of species by county. Counties are political units that, in Colorado, typically do not follow the contours of natural features and are not necessarily an appropriate size unit for delineating ranges. Because of this and because the range tool was intended to be used in a next generation gap analysis project (the Southwest Regional Gap Analysis Project), the range units selected for range delineation were eight digit "hydrologic units" from the USGS Hydrologic Unit Maps (Seaber et al. 1987). Hydrologic units (hydro-units) are sub-units of major river watershed basins. Each hydro-unit is identified by a unique hydrologic unit code (HUC) consisting of two to eight digits based on the four levels of classification in the hydrologic unit system. The eight digit HUC is the smallest element in the hierarchy of hydrologic units that was available nationwide (Figure 5).

Evidence of species occurrence was used to code hydro-units as to whether they were considered part of a species' geographic range or not. Some of the evidence for range extent came from previous species occurrence maps by county, which were overlaid on the hydro-unit map. If a county of known or likely species occurrence intersected a hydro-unit, the hydro-unit was coded as "known or likely" occurrence. Other evidence came from known location data for species. Known locations of species occurrences were obtained from the Colorado Breeding Bird Atlas (Kingery 1998), the North American Breeding Bird Survey (Sauer 2003), Latilong distribution studies (Hammerson and Langlois 1981; Bissell and Dillon 1982; Kingery 1987), bat census data (Navo 1994), Colorado amphibian and

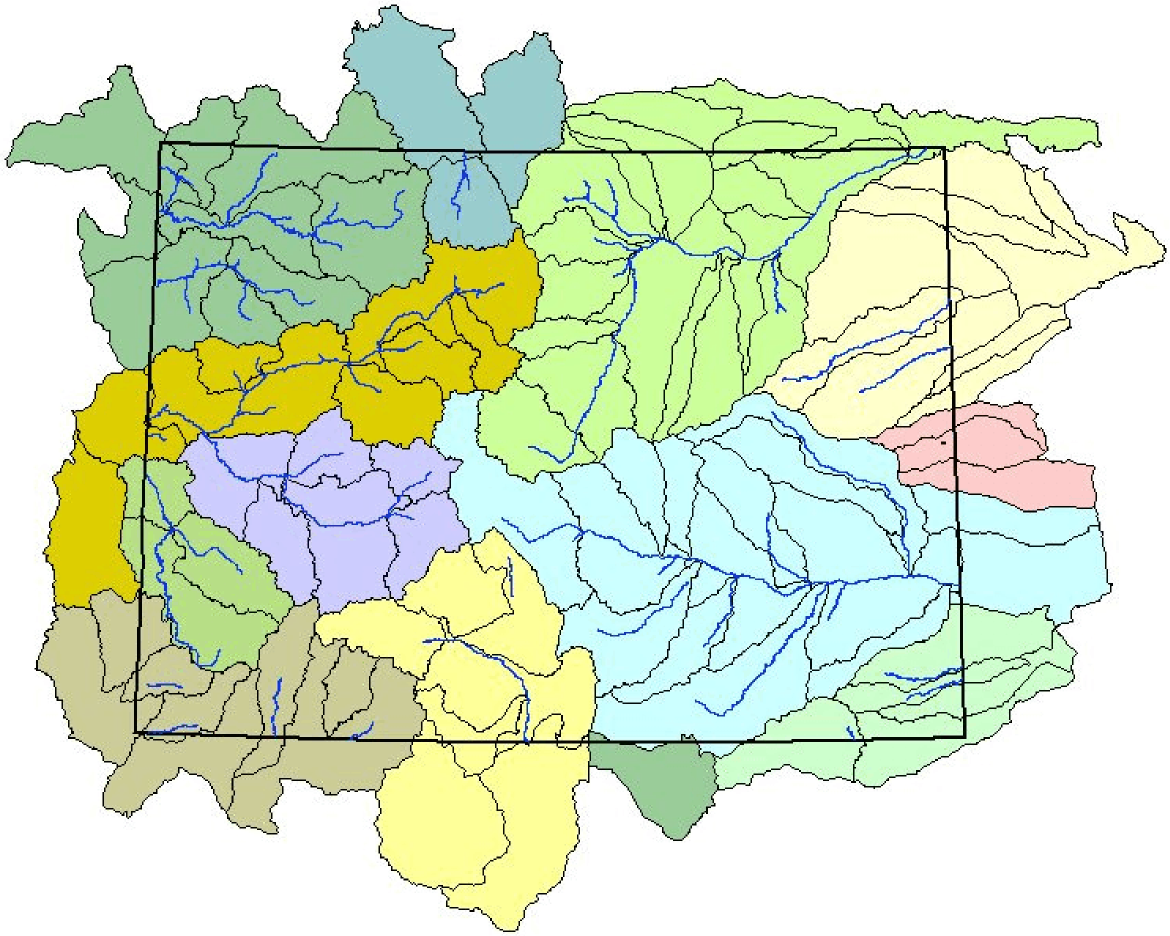


Figure 5. Colorado Hydrologic Units. The major river basins in Colorado (colors) subdivided into USGS hydrologic units, which were used to delineate geographic ranges for terrestrial wildlife species.

reptile surveys and scientific collection reports. Point locations from these sources were overlaid on the hydro-unit range maps; hydro-units where the points coincided were coded with the occurrence data. Hydro-units were then shaded according to how much evidence there was in each to support that hydro-unit being included in the species range. Lighter shades represented weaker evidence of species occurrence and darker shades represented stronger evidence of species occurrence. [Because what is being modeled is the distribution of suitable habitat and not species occurrence, species occurrence is being used here as an indicator of suitable habitat. There are potential problems with that assumption (Van Horne 1983; Pulliam 1988), which are the same problems with using species occurrence to determine species habitat affinities; however, in this case species occurrences are not being used to determine suitable habitat. Rather, they are used as evidence of the geographic extent of the habitat.] The shaded hydro-units were shown to species experts as evidence to-date of species ranges and "over-written" with the expert's knowledge.

The ArcView Species Range Review Tool includes a "pre-populated" hydro-unit range map for each terrestrial, vertebrate species in Colorado (Figure 6). The tool includes several methods to locate the user's species of interest. Once a species is selected, the species expert can review the range extent evidence collected up to the date of the review and add their opinions, in the form of elicited probabilities, on the range extent of the species. The value that the experts enter reflects two forms of uncertainty: the uncertainty associated with the distribution of the species and the uncertainty associated with the reviewer's level of knowledge about the species.

These sources of uncertainty are combined with all sources of uncertainty in the model using Bayes' Theorem and ultimately reflect the state of knowledge about the distribution of suitable habitat for the species. The instructions for the Range Review Tool are displayed in Appendix A. They prompt the species experts to review the range maps and add their opinions about the range of the species by selecting hydro-units and providing a value for how certain they are that species habitat is found in the selected hydro-units. The values entered must be between 0 and 1 inclusive, with 0 meaning that they are absolutely certain habitat is not found in the hydro-unit and 1 meaning that they are absolutely certain that habitat is found in the hydro-unit. The values are captured in database tables and as ArcView polygon "shapefiles" (Figure 7). The shapefiles are then converted to raster grids and used in the Bayesian calculations of uncertainty.

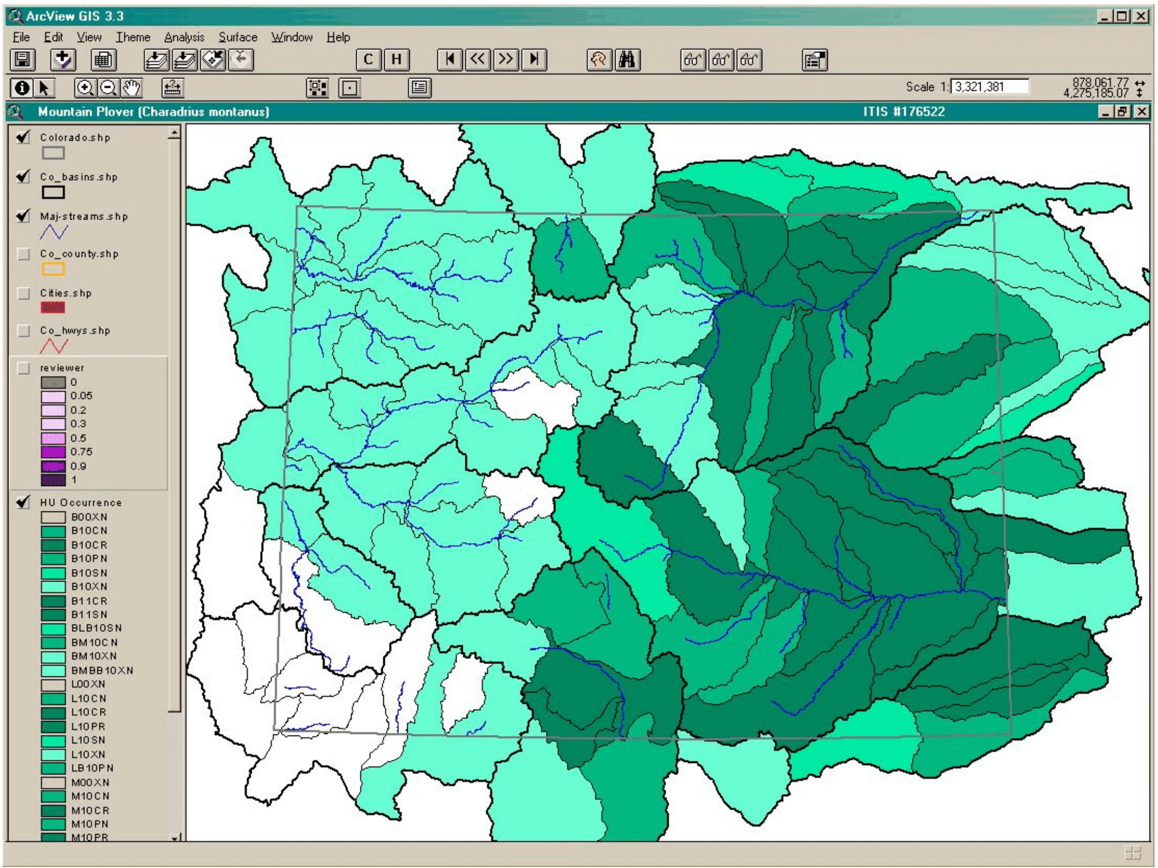


Figure 6. ArcView Species Range Review Tool with Preliminary Data. ArcView tool used by species experts to review and input opinions on species geographic ranges, showing shaded hydro-units representing the strength of evidence for species occurrence.

The next tool developed was designed so that species experts could review the individual parameters of the wildlife habitat relationships and add their opinions on the certainty of these relationships. This tool was developed using Microsoft Excel. The user selects a species from a drop-down list and the binary parameter values (1's or 0's) that went into the original model for that species appear in the spreadsheet. The species experts then add their opinions, again in the form of elicited probabilities, as to the certainty of the relationships (Figure 8). The probability values are saved in a separate spreadsheet when

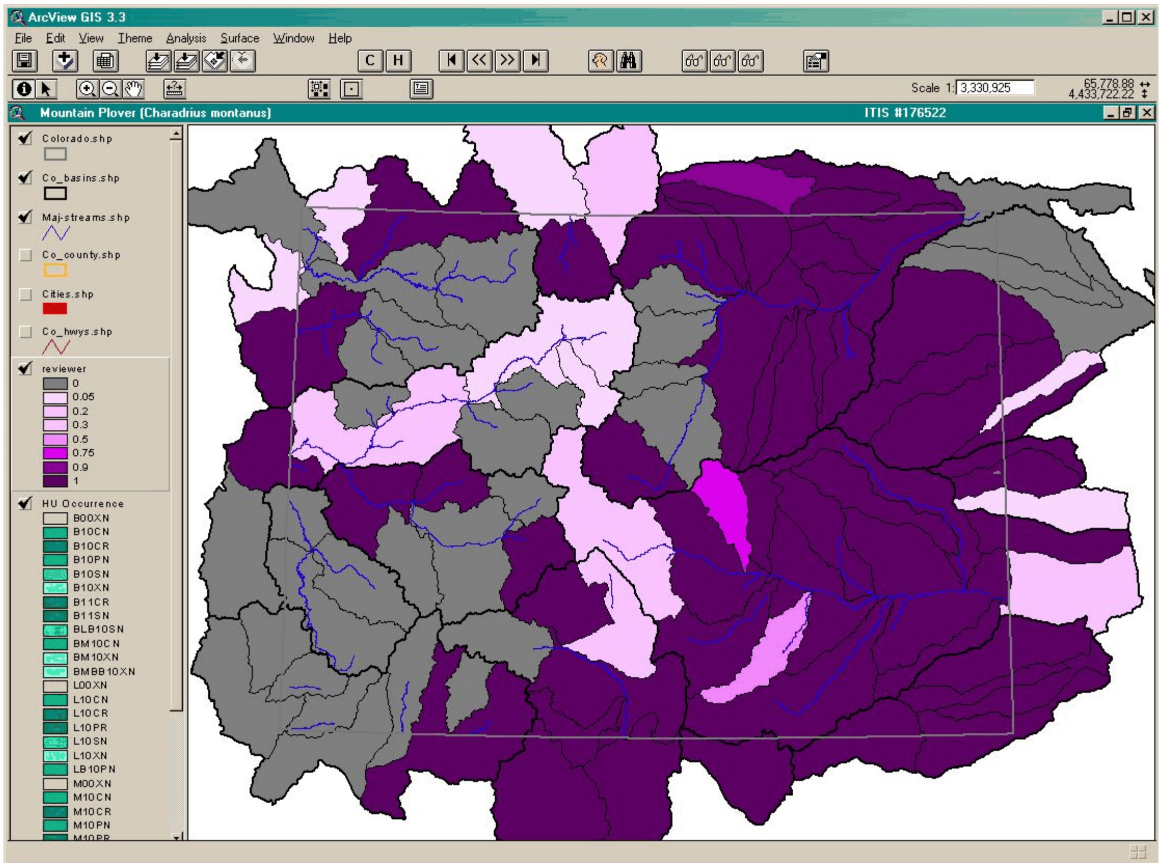
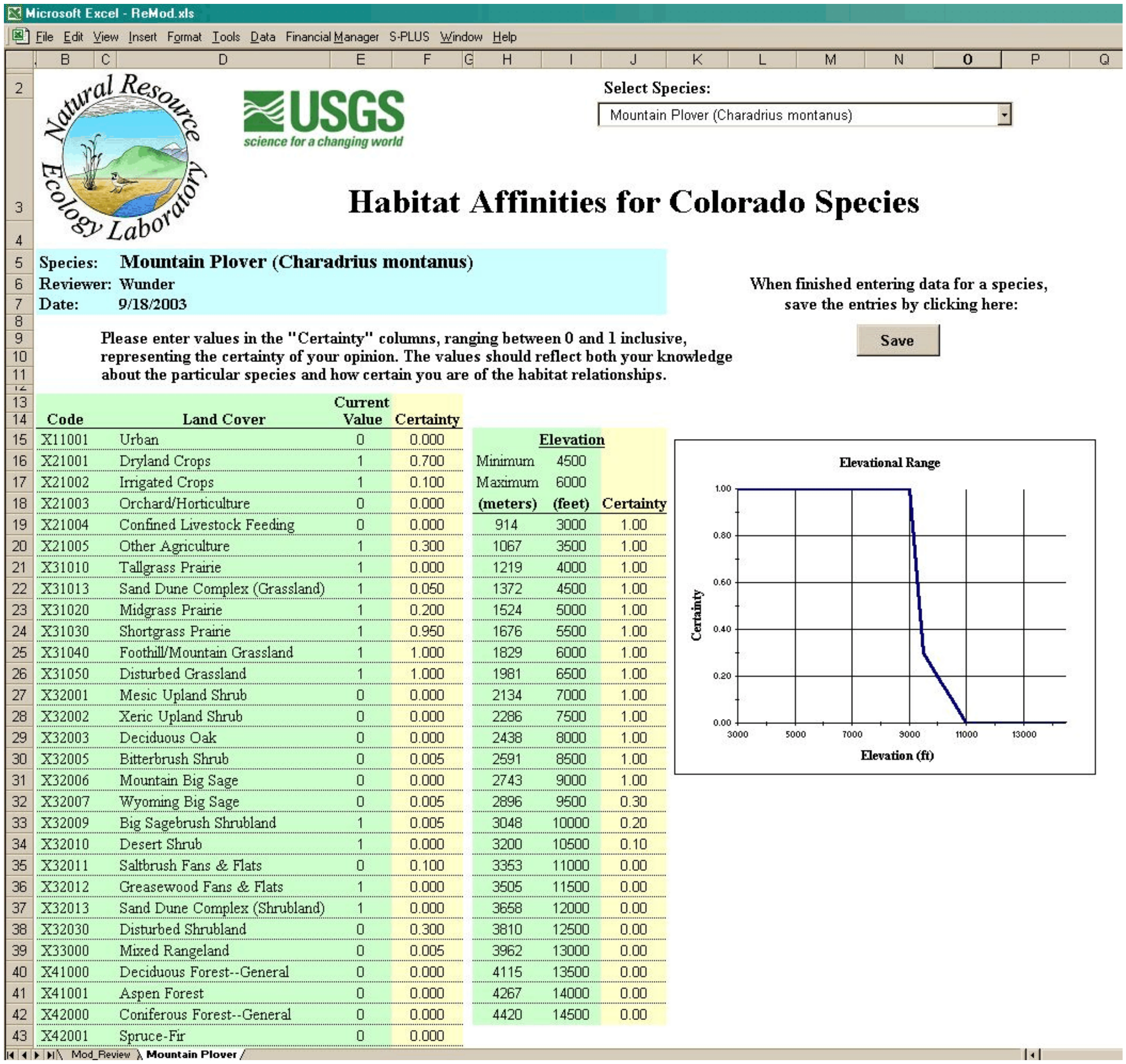


Figure 7. ArcView Species Range Review Tool with Probabilities. ArcView tool used by species experts to review and input opinions on species geographic ranges, showing example of opinions given as probabilities of occurrence. Probabilities are mapped over the preliminary data.

the “Save” button is clicked. The spreadsheets are converted to (.dbf) database tables and imported into ArcView and used to re-code the raster data layers used in the original habitat model to produce probability surfaces.

The first iteration of the habitat and range review tools were evaluated by colleagues and species experts and modified for ease of understanding and use. Originally the model review tool was developed in ArcView with a function to find the prior habitat model, view the predicted habitat map, collect expert opinions on model parameters and rerun the model



Microsoft Excel - ReMod.xls

Select Species: Mountain Plover (Charadrius montanus)

Habitat Affinities for Colorado Species

Species: Mountain Plover (Charadrius montanus)
Reviewer: Wunder
Date: 9/18/2003

When finished entering data for a species, save the entries by clicking here: Save

Please enter values in the "Certainty" columns, ranging between 0 and 1 inclusive, representing the certainty of your opinion. The values should reflect both your knowledge about the particular species and how certain you are of the habitat relationships.

Code	Land Cover	Current Value	Certainty
X11001	Urban	0	0.000
X21001	Dryland Crops	1	0.700
X21002	Irrigated Crops	1	0.100
X21003	Orchard/Horticulture	0	0.000
X21004	Confined Livestock Feeding	0	0.000
X21005	Other Agriculture	1	0.300
X31010	Tallgrass Prairie	1	0.000
X31013	Sand Dune Complex (Grassland)	1	0.050
X31020	Midgrass Prairie	1	0.200
X31030	Shortgrass Prairie	1	0.950
X31040	Foothill/Mountain Grassland	1	1.000
X31050	Disturbed Grassland	1	1.000
X32001	Mesic Upland Shrub	0	0.000
X32002	Xeric Upland Shrub	0	0.000
X32003	Deciduous Oak	0	0.000
X32005	Bitterbrush Shrub	0	0.005
X32006	Mountain Big Sage	0	0.000
X32007	Wyoming Big Sage	0	0.005
X32009	Big Sagebrush Shrubland	1	0.005
X32010	Desert Shrub	1	0.000
X32011	Saltbrush Fans & Flats	0	0.100
X32012	Greasewood Fans & Flats	1	0.000
X32013	Sand Dune Complex (Shrubland)	1	0.000
X32030	Disturbed Shrubland	0	0.300
X33000	Mixed Rangeland	0	0.005
X41000	Deciduous Forest--General	0	0.000
X41001	Aspen Forest	0	0.000
X42000	Coniferous Forest--General	0	0.000
X42001	Spruce-Fir	0	0.000

Elevation

Minimum 4500
Maximum 6000

(meters)	(feet)	Certainty
914	3000	1.00
1067	3500	1.00
1219	4000	1.00
1372	4500	1.00
1524	5000	1.00
1676	5500	1.00
1829	6000	1.00
1981	6500	1.00
2134	7000	1.00
2286	7500	1.00
2438	8000	1.00
2591	8500	1.00
2743	9000	1.00
2896	9500	0.30
3048	10000	0.20
3200	10500	0.10
3353	11000	0.00
3505	11500	0.00
3658	12000	0.00
3810	12500	0.00
3962	13000	0.00
4115	13500	0.00
4267	14000	0.00
4420	14500	0.00

Figure 8. Habitat Relationship Review Tool. MS Excel tool used by species experts to review and input opinions on the certainty of species habitat relationships.

with new parameters. This program became too complex and unwieldy and the time to rerun models was too long for efficient review sessions.

The habitat review tool was redesigned in Microsoft Excel. This tool allowed the experts to find the prior model parameters (not mapped habitat) and add their opinions about their certainty of the habitat relationships. Hard copies of prior habitat maps were provided at the sessions, if the reviewers requested them. No attempt was made to run the new calculations at the review sessions. This reduced the time and complexity involved in reviewing species habitat relationships considerably. The tool does include built-in “pop-up” descriptions of landcover types and landcover distribution maps.

The data review/collection tools were presented at several wildlife meetings (i.e., Western Bat Working Group, Colorado Division of Wildlife Habitat Section, Gap Analysis Habitat Workshop) and valuable feedback on their use and the interest of species experts was received.

The datasets reviewed and used in the models varied by species. Possible data layers included: landcover, elevation, streams, lakes and geographic ranges (Table 1). Derivative datasets such as aspect, slope, modeled riparian areas and proximity to water were potential additions to the models, if experts specified these as important. The base maps were re-coded with the probability values obtained from the expert reviews to derive raster probability surfaces for each parameter included in the habitat models (Table 2).

Table 1. Data Layers Used in Habitat Models.

Data Layer	**Source**	**Series**	**Date**	**Scale**
Elevation	USGS	Digtal Elevation Model	1996	90 m
Streams	USGS	Digital Line Graph	1994	1:100,000
Lakes	USGS	Digital Line Graph	1994	1:100,000
Hydrologic Units	USGS	Hydrologic Unit Maps	1996	8 digit HUC
Landcover	Colorado GAP	Classified Landsat Images	2000	30 m

Figure 9 displays the raster GIS landcover map developed by Colorado GAP (Schrupp et al. 2000). Figure 10 shows this layer re-coded as a probability surface, reflecting one expert’s assessment of the uncertainty inherent in the relationship between landcover and suitable habitat for mountain plover. Similarly, Figure 11 shows the raster GIS elevation dataset, and Figure 12 shows this grid re-coded to reflect expert assessment of the uncertainty in the relationship between elevation and suitable habitat for mountain plovers. The explicit steps used to convert the grid datasets to probability surfaces are listed in Appendix B.

Table 2. Re-Code Table for Grid Layer Values to Probabilities. An example of the tables used to re-code habitat element grid cells to probability values.

Landcover Type	LC Code	Certainty	Grid Value
Shortgrass Prairie	X31030	0.01	10
Foothill/Mountain Grassland	X31040	0.03	30
Mesic Upland Shrub	X32001	0.6	600
Deciduous Oak	X32003	0.03	30
Bitterbrush Shrub	X32005	0.05	50
Mountain Big Sage	X32006	0.05	50
Saltbrush Fans & Flats	X32011	0.02	20
Greasewood Fans & Flats	X32012	0.02	20
Sand Dune Complex (Shrubland)	X32013	0.01	10
Aspen Forest	X41001	0.7	700
Douglas Fir	X42003	0.8	800
Lodgepole Pine	X42004	0.75	750
Blue Spruce	X42011	0.8	800
Juniper	X42015	0.6	600

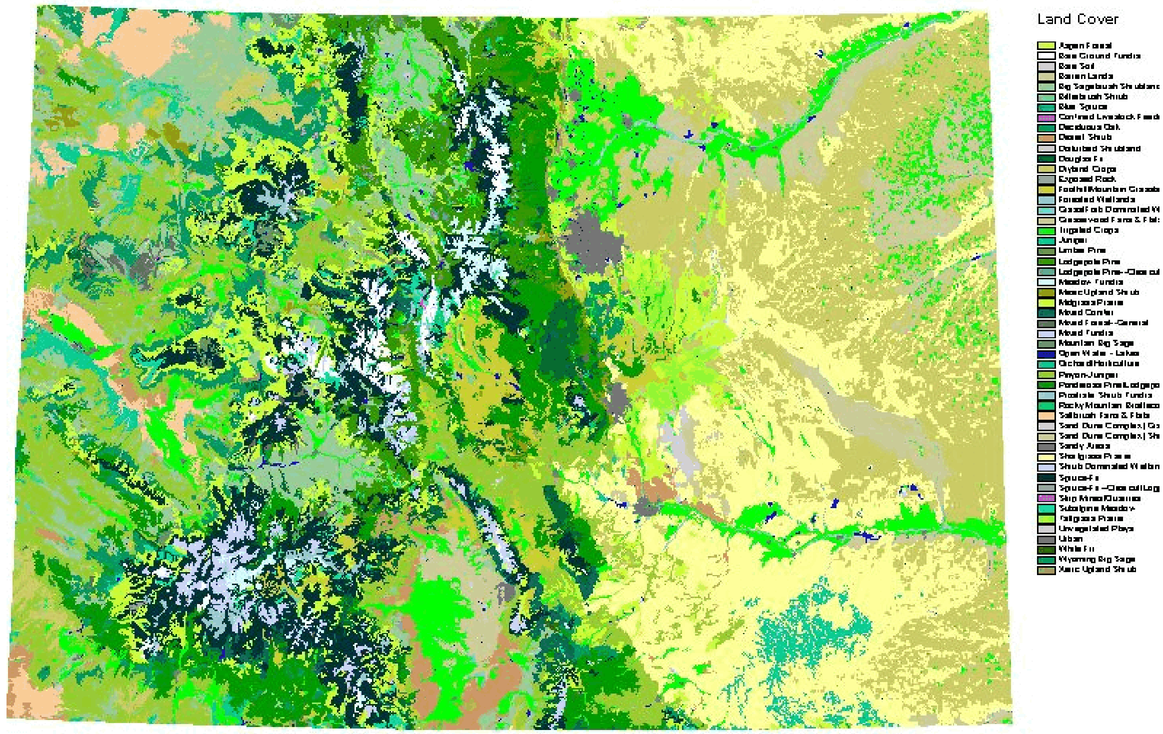


Figure 9. Colorado Landcover Map. The raster GIS landcover map developed by the Colorado Gap Analysis Project (Schrupp et al. 2000).

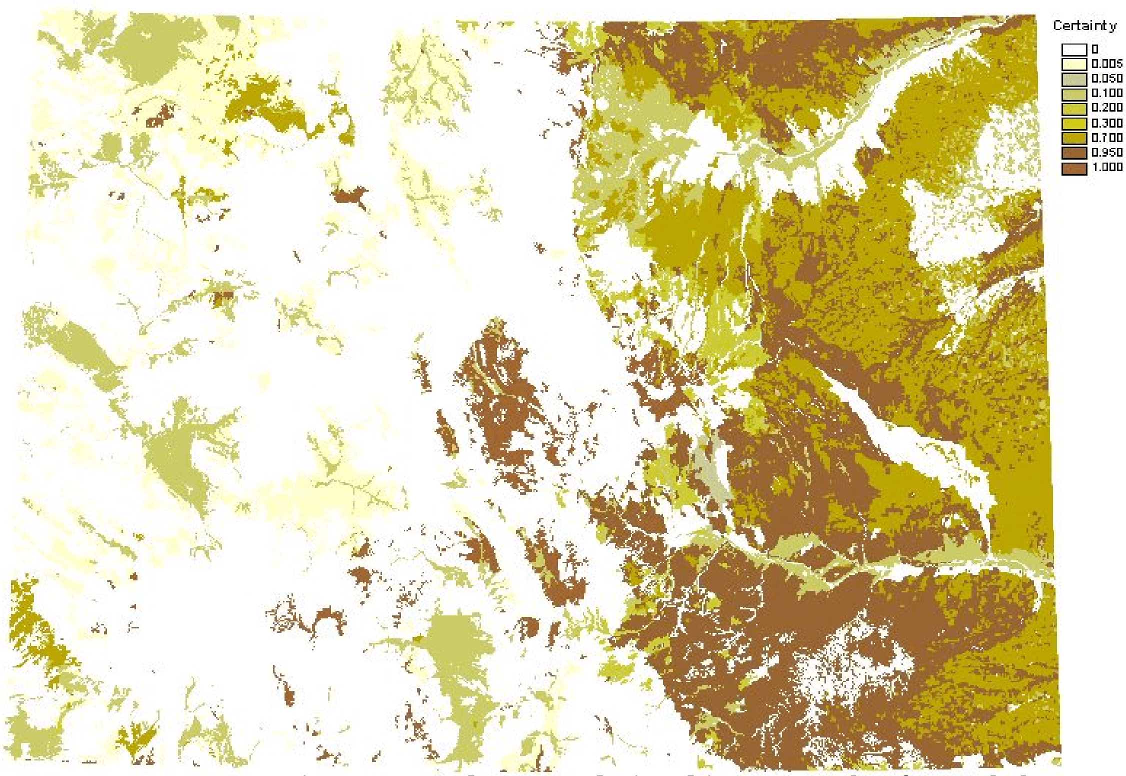


Figure 10. Expert Certainty on Landcover Relationships. Example of re-coded landcover grid using probabilities obtained from species expert on the certainty of landcover relationships for the mountain plover.

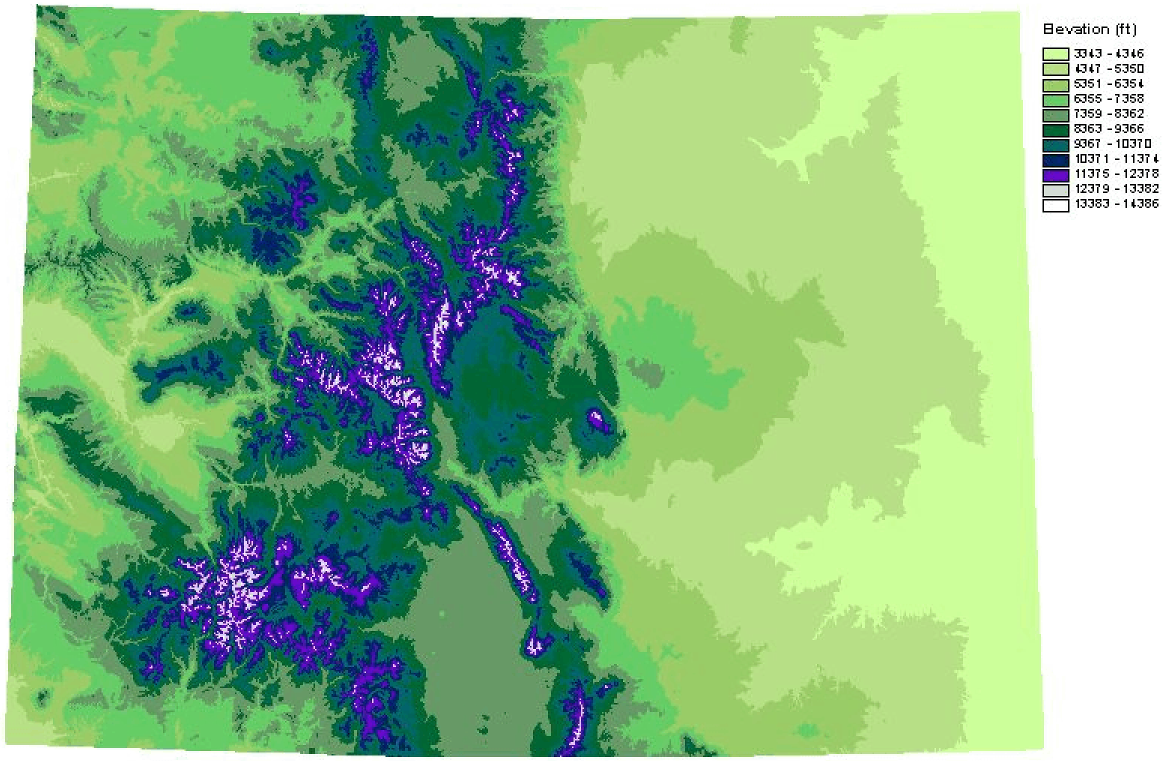


Figure 11. Colorado Elevation Raster Map. Elevation map developed from the USGS digital elevation models in 90m raster format.

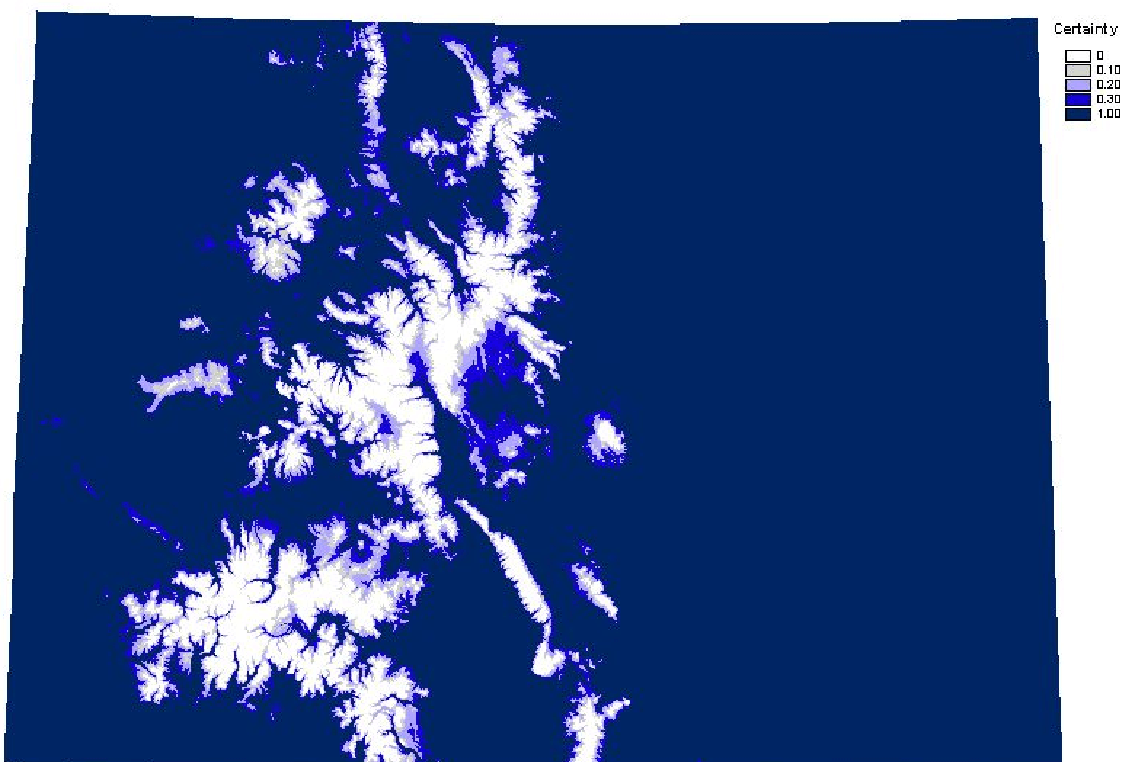


Figure 12. Expert Certainty on Elevational Relationships. Example of re-coded elevation grid using probabilities obtained from species expert on the certainty of elevational relationships for the mountain plover.

Applying Bayes' Theorem

Raster probability surfaces were combined using Bayes' Theorem in ArcView, so that a posterior probability value was calculated for each pixel based upon the value of that pixel in each layer used in the model. Bayes' Theorem calculates a conditional posterior probability based upon the prior probability and an updating likelihood function. The calculation used in each grid cell is:

$$P(S|R) = \frac{P(S) * P(R|S)}{P(S)*P(R|S) + (1-P(S)*1-P(R|S))}$$

Where:

P(S) = probability of habitat being suitable (prior probability)
P(R|S) = probability of habitat relationships given probability that habitat is suitable (averaged across habitat elements and experts)
P(S|R) = probability of habitat being suitable given probabilities of habitat relationships (posterior probability)

An ArcView script was written that automates the Bayes' calculation and queries for the layers to be included in the model. The script can be found in Appendix C. The Bayesian calculation used to combine the data layers looks like this as ArcView Avenue script:

```
postGrid  =   ( priorGrid * suitGrid * int.AsGrid ) ÷
            (( priorGrid * suitGrid ) + ( unpriorGrid * unsuitGrid ))
```

where *postGrid* is the resulting posterior probability surface; *priorGrid* is the previous habitat model converted to a probability surface; *suitGrid* is the habitat suitability probability surfaces from each expert averaged together; *int.AsGrid* is the conversion factor used to convert probabilities to whole numbers (1000 in this case); *unpriorGrid* is one minus the *priorGrid*; and *unsuitGrid* is 1 minus the values in each of the habitat suitability probability surfaces averaged together.

The numerator of the equation is multiplied by 1000 so that the cell values in the final probability surface calculate to whole numbers, and the grid cells in the denominator are subtracted from 1000 instead of one, because they had earlier been multiplied by 1000. The new data layer probability grids that are used to “update” the prior probability surface (previous model) are averaged together. However, the landcover grid is given twice the weight in the average because it is the driving data layer in the models, whereas the range and elevation layers do not necessarily predict where suitable habitat will be; they instead act as constraints on the distribution of habitat. So the equations for habitat grids are:

suitGrid = elevation grid * range grid * (2x landcover grid) ÷ 4

unsuitGrid = (1-elevation grid) * (1-range grid) * (2x (1-landcover grid)) ÷ 4

The result of this calculation is a posterior probability surface, with each cell depicting the cumulative uncertainties (probabilities) of the knowledge-based habitat relationship data that were used in the model (Figure 13).

Landcover Classification Uncertainty

Other sources of uncertainty in wildlife habitat suitability models are the classification and spatial inaccuracies in the data layers used to create the models (Dean et al. 1997; Flather et al. 1997). To account for these sources of uncertainty, the results of an accuracy assessment of the landcover map (Reiners et al. 2000) were included in the overall uncertainty of the habitat predictions. Reiners et al. (2000) conducted an accuracy assessment of the Colorado GAP landcover map using air videography to determine the accuracy of the classification of each landcover class. As part of the accuracy assessment, they conducted a fuzzy accuracy assessment assigning degrees of rightness and wrongness to map units based on the seriousness of the error with regard to animal habitat models (Gopal and Woodcock 1994). The assumption of classical (crisp) set theory for traditional

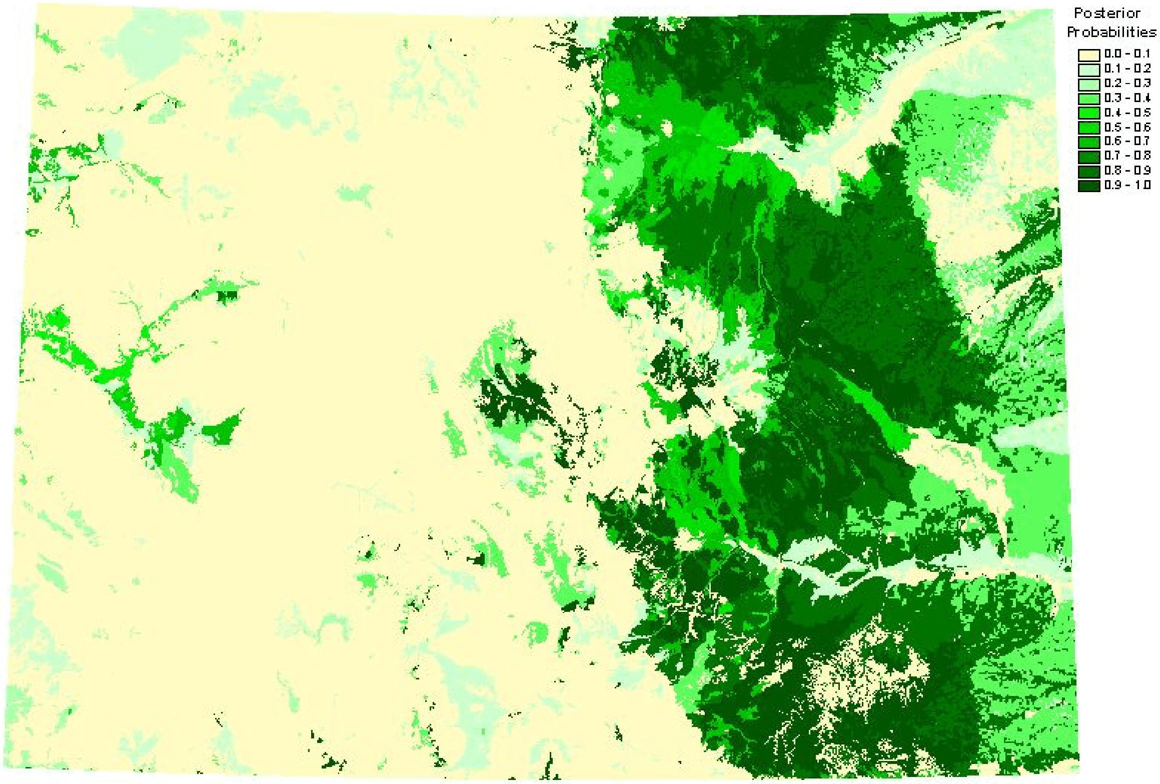


Figure 13. Posterior Probability Surface. An example of a posterior probability surface depicting the cumulative uncertainty in the mountain plover habitat suitability model based upon the elicited opinions of a species expert.

accuracy assessment is that classified map units are either completely and unambiguously correct or equally incorrect. Fuzzy set theory, in contrast, uses degrees of set membership. For the Colorado GAP landcover map, they conducted fuzzy accuracy assessment by recognizing that some map errors have more serious consequences for animal habitat models than others. By quantifying this "seriousness" using a coded verbal scale, they were able to measure several aspects of accuracy. The “RIGHT” operator (Gopal and Woodcock 1994) is perhaps the most intuitive of the fuzzy operators that were used. With this operator, codes were assigned representing a verbal "correctness" scale by judging the seriousness of mismatches between the classified map and the reference data in the context of the GAP habitat suitability models. The proportion of matches by this criterion is the measure of accuracy of the mapped cover types when errors considered acceptable for habitat modeling are counted as correct, even if they are not perfect answers. Overall map accuracy for the Colorado landcover map using the RIGHT criterion is 75.7%. This accuracy reflects information about the frequency of errors with regard to animal habitat modeling not expressed in user's accuracy (Gopal and Woodcock 1994).

The results of the RIGHT fuzzy assessment are on a scale of 0 to 1 and have a similar interpretation as probabilities. Fuzzy values were converted directly to probabilities of accurate classification for each landcover class (Appendix D). There were 14 “NA” results out of 52 landcover classes. "NA" indicates that an accuracy assessment was not done for that type.“NA” were converted to “non-informative” probability values of 0.5. The Colorado landcover map was then re-coded with the probabilities to create a landcover accuracy probability surface (Figure 14).

This surface was then multiplied by the posterior probability maps for each species habitat model (Figure 15). The probabilities were multiplied because, for all landcover accuracy probabilities less than one, the desired result is that certainty is decreased. A landcover accuracy probability of 1 does not change the level of uncertainty of the predicted habitat distribution. However, if the accuracy of the landcover classification is in doubt (probability of less than 1), then uncertainty in predicted habitat distribution should increase. This way, areas with low certainty of being suitable habitat (probabilities near 0) cannot have increased probabilities of being suitable habitat merely because the landcover classification for that area was accurate. Landcover classification inaccuracy can only decrease the probability of predicting distribution of suitable habitat, it cannot increase it.

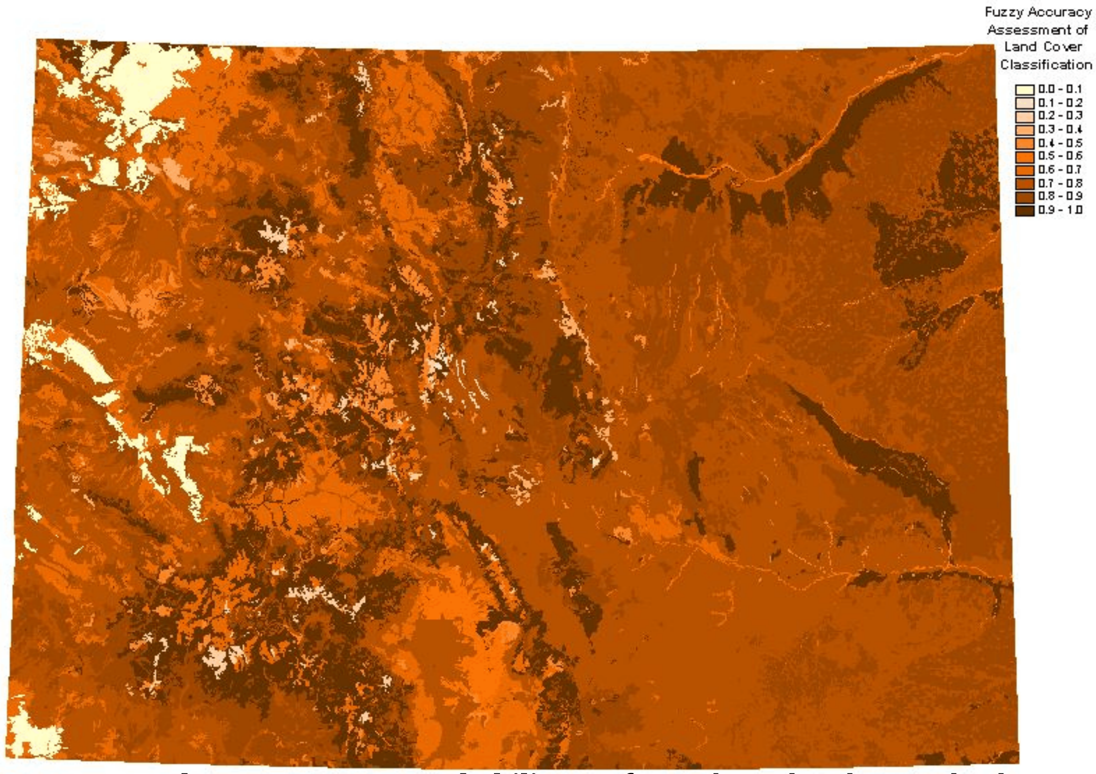


Figure 14. Landcover Accuracy Probability Surface. The Colorado GAP landcover map re-coded with RIGHT fuzzy operator values converted to probabilities, representing accuracy probabilities for each landcover class.

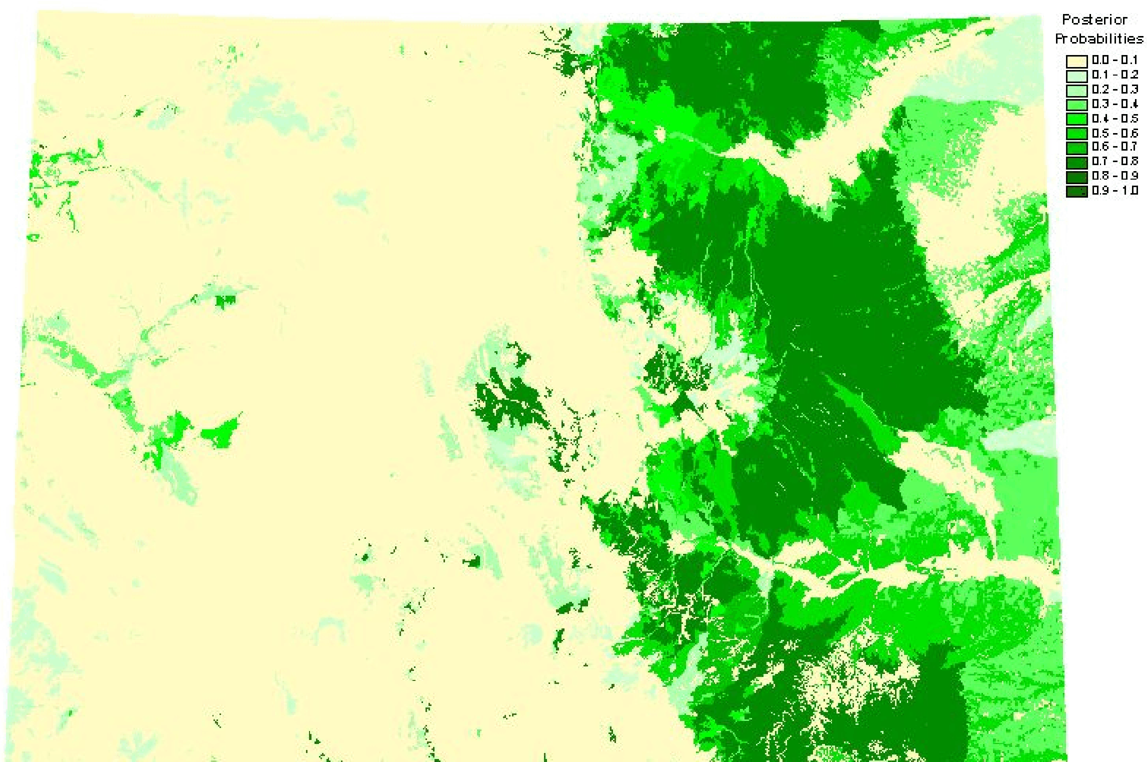


Figure 15. Posterior Probability and Landcover Uncertainty. An example of a posterior probability surface combined with uncertainty in the landcover classification.

Combining Opinions of Several Experts

The next step in the study (Case #2 on flowchart, Figure 2) was to obtain opinions from several experts about a single species' habitat relationships and combine all the data layer probability surfaces from each expert into a single posterior probability surface, depicting the "state of knowledge" about the distribution of suitable habitat for the species. The species selected for this analysis was the boreal toad (*Bufo boreas*), because the species is endangered and well studied, and there are many experts on its habitat affinities and range in Colorado.

Suitable habitat for the boreal toad includes proximity to water as a predictive element, so a water proximity data layer was created by starting with a map of all the lakes and streams in the state. The Colorado stream and lake maps came from the USGS 1:100,000 scale digital line graph (DLG) series. The streams map had been topologically "cleaned up" for the Colorado GAP project by connecting all the stream segments (Schrupp et al. 2000). The streams and lakes were buffered in 100 m intervals out to a total distance of 1000 m (Figure 16). The total distance of the buffers from open water could be extended, however, the process requires a computer with more memory than was available for this study. According to boreal toad experts, 1000 m was sufficient to describe this species' suitable habitat.

Species experts were asked to state how certain they were that suitable habitat for the boreal toad occurred at each interval away from open water. The MS Excel habitat affinity tool collected the responses (Figure 17) and created a graphic representation of the proximity to water habitat function as the responses were entered. The data collected from these responses was used to re-code the proximity to water grid with the experts' degree of

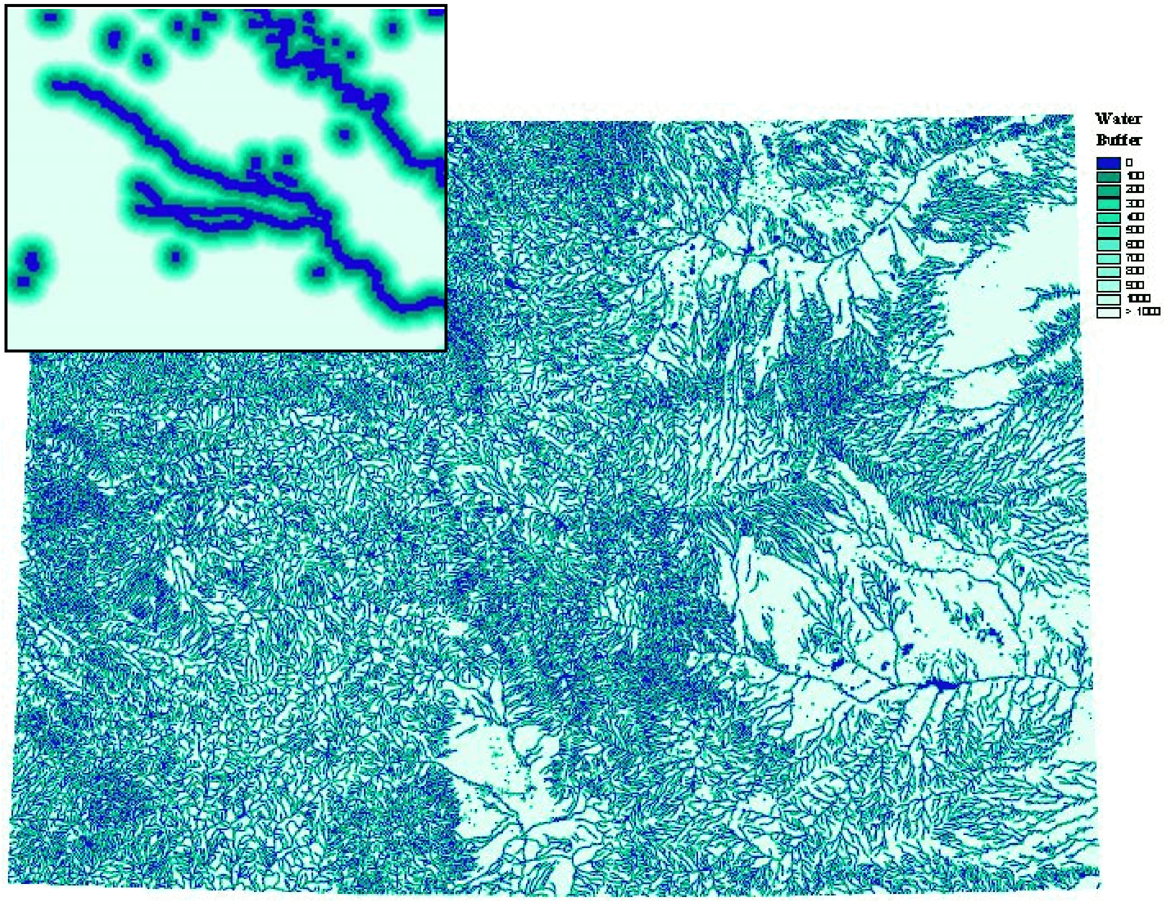


Figure 16. Colorado Proximity to Water Map. Map developed by creating 1000 m buffers (in 100 m intervals) around all open water features. Insert shows enlarged area.

certainty that each interval was associated with suitable habitat for the boreal toad. This probability surface was then added into the Bayesian calculation to produce a probability surface of suitable habitat for each expert.

Six experts were approached to participate and give their opinions on their certainty of habitat distribution and habitat affinities for the boreal toad. A posterior probability surface of suitable habitat was created from the responses of each expert for comparison, using the Bayesian calculations previously mentioned. Then an overall calculation was made, averaging the responses of all experts into one probability surface. The resulting

Is distance from water a factor in suitable habitat for this species?

Y

Distance from Water		
(meters)	(feet)	Certainty
0	0	1.00
100	328	1.00
200	656	0.95
300	984	0.85
400	1312	0.70
500	1640	0.50
600	1969	0.35
700	2297	0.20
800	2625	0.10
900	2953	0.04
1000	3281	0.01
1100	3609	0.00

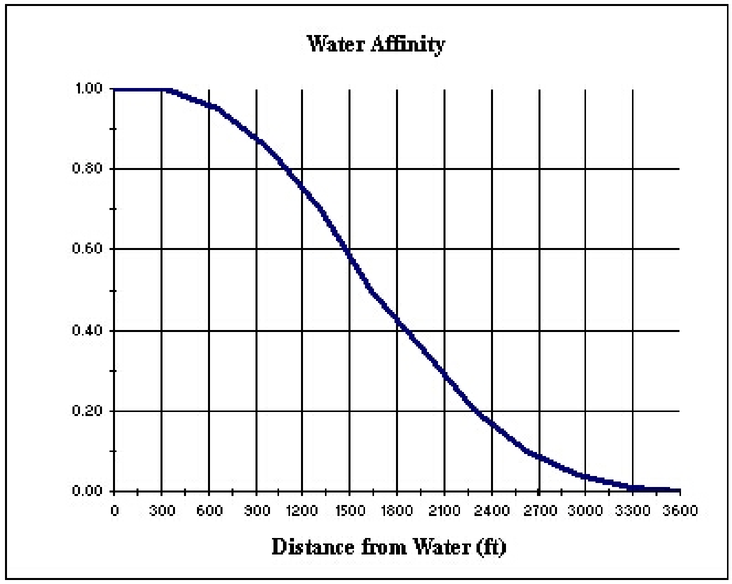


Figure 17. Proximity to Water Data Collection Tool. This is a section of the MS Excel habitat review tool that collects expert certainty on the relationship of suitable habitat to the proximity to open water.

overall posterior probability surface was then multiplied by the landcover classification fuzzy accuracy assessment probability surface to depict the overall uncertainty in the boreal toad model.

Modeling Functional Landscapes

To examine how landscape context could be introduced into these models, an example using the Colorado GAP lynx habitat model and some hypothetical landscape metrics was developed (Case #3 on flowchart, Figure 2). Expert opinion was collected on the standard data layers in the model. Then, to assess the effect of minimum patch size restrictions on the model, probabilities were assigned to different patch sizes based upon what may constitute preferred patch size for the lynx. Ideally this would be done by a species expert who has knowledge of how the species uses habitat in a landscape, but the values were estimated here to serve as a test of the methods. The patches were divided into six different sizes from very small to very large and assigned probabilities (Table 3). A data layer was then created with the potential lynx habitat patches re-coded with their probability of being suitable based upon their size (Figure 18). This layer was incorporated into the Bayesian calculation to produce a map that had lower probabilities of being suitable for habitat patches that were smaller. This same procedure could be used with other landscape metrics, assigning probabilities of the habitat being suitable based upon isolation of patches, connectivity, or juxtaposition with other habitat types.

Table 3. Probabilities Assigned to Lynx Habitat Patch Sizes.

Patch Size (ha)	Probability Assigned
0	0.0
1 - 2000	0.01
2001 - 5000	0.1
5001 - 10,000	0.5
10,001 - 50,000	0.8
50,001 - 600,000	1.0

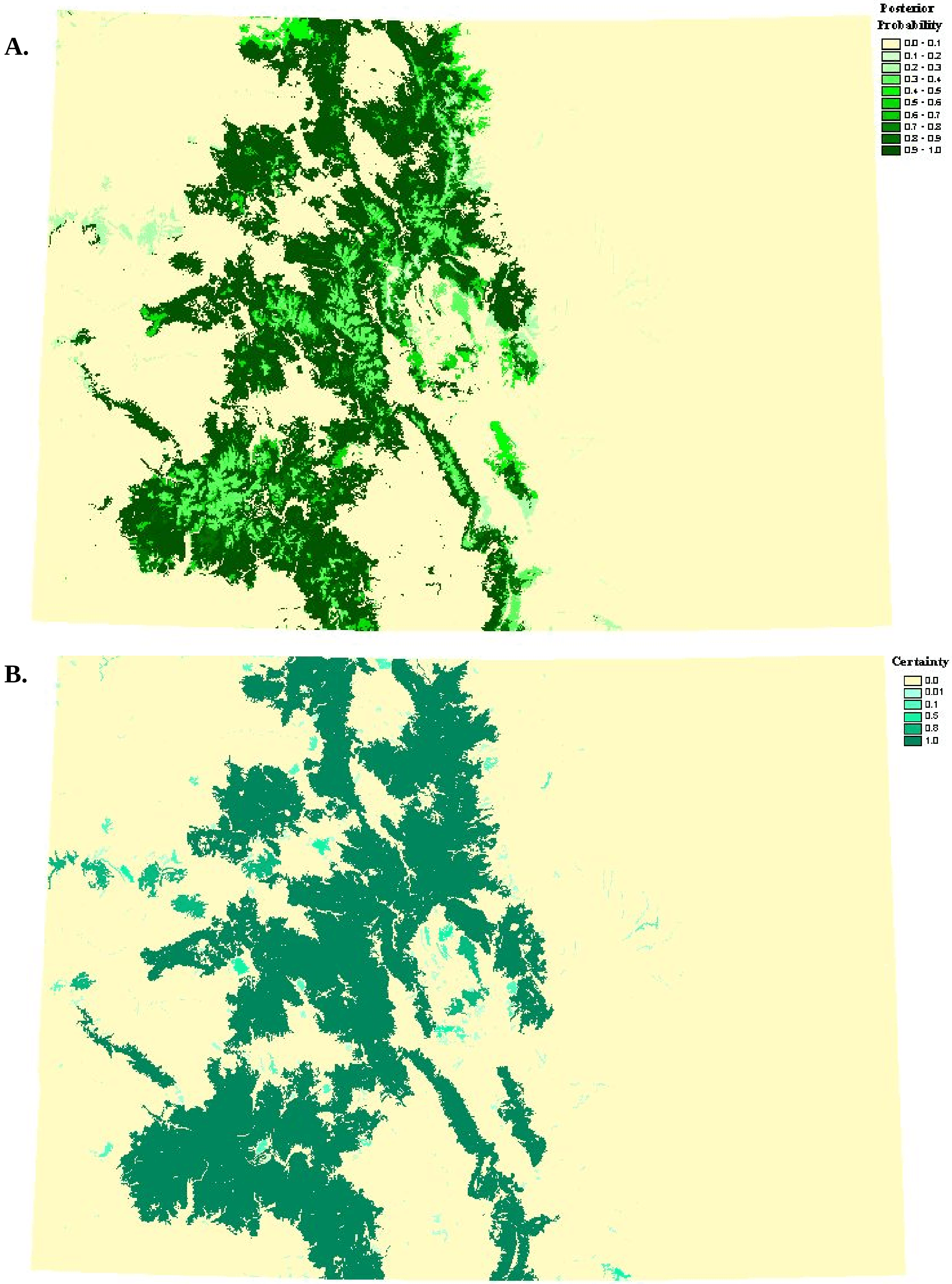


Figure 18. Hypothetical Lynx Habitat Patch Size Probability Surface. Potential lynx habitat patches from the Bayesian model (A) re-coded to six probability categories based upon patch size (B).

Sensitivity Analysis

Bayes' Theorem relies upon the information contained in a subjective prior probability. Therefore the influence of the prior upon the results is important to ascertain and disclose. The final step of this study tests the sensitivity of the habitat models to the influence of prior probabilities. Three different methods for testing sensitivity were carried out. The effects on the model of assigning different prior probabilities were examined by holding 2 of the 3 prior probability assignments (0.1, 0.5 and 0.6 respectively for non, potential and likely habitat) constant, while allowing one probability to change over a range of values. In addition, all three prior probability values were assigned a single probability value that was allowed to change over a range of possible values. Another analysis was done by assigning an area of the prior probability surface an "erroneous" probability value and calculating posterior probabilities with 1 through 5 expert opinions to determine how well updating with new "accurate" information corrected the models.

Other assumptions were tested for their effects on the model. The effects of doubling the weight of the landcover layer compared to other data layers was compared to treating all data layers as the same weight. The effects of an expert assigning a non-informative probability (0.5) to areas where they feel they do not have the expertise to judge suitable habitat were examined. Finally, for models incorporating the opinions of several experts, the method of combining species opinions by averaging them together and using Bayes' Theorem to combine the average with the prior was compared to using the outcome of the first expert's opinion as the prior in Bayes' Theorem combining it with the second expert and so on using each outcome as the prior for the next iteration, then reversing the order.

RESULTS

Using a model to understand and solve problems positively requires that all who use it understand it.

– Anthony Starfield 1997

The main goal of this study was to develop a method to derive habitat suitability models that are easy to understand, credible, and easy to develop using species expert opinions. As such, the time involved and the ease or difficulty of collecting the required information from experts in the correct format and the ease or difficulty of developing the models was important to ascertain.

All the species experts that were asked participated in the study. Individual review sessions were arranged with 6 different species experts and 2 agreed to do the reviews on their own after acquiring the review tools via e-mail. Each session started by explaining the goals of the study, the procedures for reviewing ranges and habitat model parameters, and the format in which the experts were to submit their opinions. The experts all grasped the purpose and procedures easily and quickly. A review session with one expert reviewing a single species range and habitat relationships, including time for describing the study and the tools, averaged about 45 minutes. The time involved to review additional species was considerably less.

In two cases the review tools were e-mailed to experts with printed instructions (Appendix A) and the experts attempted to conduct the reviews without assistance. In the first attempt the tools did not work correctly because of software version incompatibilities and macro security settings. I was not available to help correct the problems at the time, so the expert recorded her opinions on paper and mailed them in. The second reviewer did not complete the review and did not provide any feedback, other than that she was very busy.

Once opinions were collected, converting them to probability surfaces and calculating posterior probabilities with Bayes' Theorem was straightforward using the procedures outlined in Appendix B and the Avenue scripts in Appendix C. It took about 45 minutes to convert opinions into probability surfaces and run the Bayesian calculations on each species.

An expert on mountain plover habitat participated to test the basic model procedures. The Colorado Gap Analysis habitat suitability map for the mountain plover was converted to a prior probability surface. Then expert opinions on landcover, elevation, and geographic range were compiled into probability surfaces and Bayes' Theorem was used to derive a posterior probability surface. The resulting posterior probability surface spatially depicts the uncertainty inherent in the habitat associations used to derive the model ranging from 0 (indicating absolute certainty of unsuitable habitat) to 1 (indicating absolute certainty of suitable habitat).

The posterior probability surface spreads the predictions of habitat suitability from 3 distinct categories to a continuous response based upon the strength of the predictions. Many areas that were classified as unsuitable habitat in the prior model are shown to have a probability of being suitable (Figure 19). These areas would have been excluded from consideration in mountain plover management and conservation plans using the existing GAP habitat model. The posterior probability surface not only shows more potentially suitable habitat for the species, but it also shows the spatial distribution of the potentially suitable habitat and it shows strengths of the predictions of this habitat.

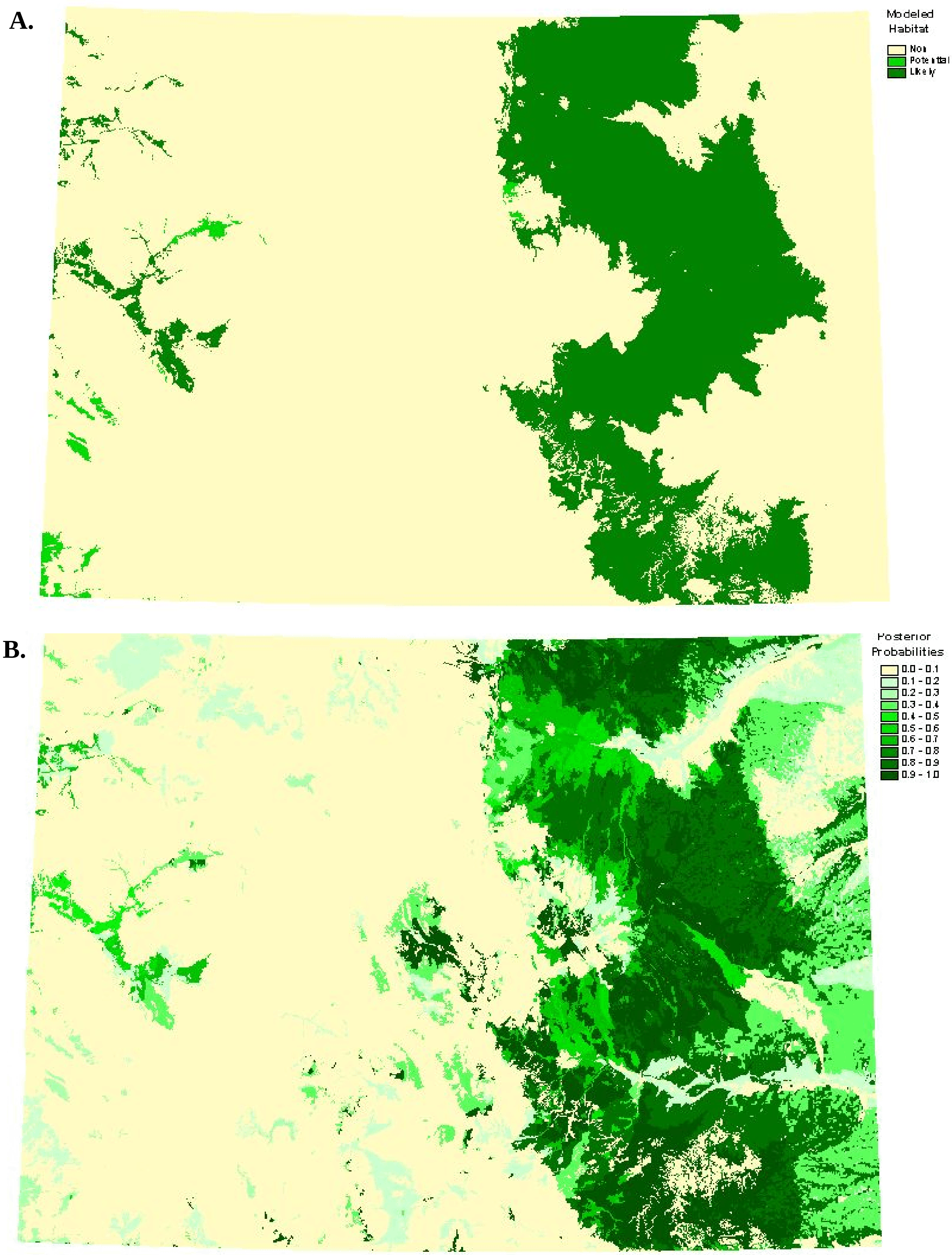


Figure 19. Prior and Posterior Probability Surfaces for the Mountain Plover. A comparison of the mountain plover prior model (A) and posterior probability surface (B). The latter depicts the cumulative uncertainty in the habitat suitability model based upon the opinions of a species expert and prior probabilities.

The change in classification of areas tended to be from areas considered non-suitable habitat to areas having some probability of being suitable (Table 4). Histograms of the area in prior habitat categories and of the area with different posterior probabilities show the distribution of areas across these categories (Figure 20). The graphs reveal the continuous and more nuanced nature of the posterior probabilities as compared to strict categories of the prior habitat model.

Table 4. Percentage of area in each category of the mountain plover prior habitat model and probabilities in the posterior probability surface.

Prior Habitat Model		Posterior Probability Surface	
Non-habitat	78.0%	Probability of being suitable < 0.3	65.4%
Potential Habitat	0.5%	Probability of being suitable 0.3-0.7	12.8%
Likely habitat	21.4%	Probability of being suitable > 0.7	21.8%

This posterior probability surface depicts the uncertainty attributed to the habitat associations that were used to build the model. It does not reflect other sources of uncertainty in the model. To ascertain how using Bayesian methods to include uncertainty in the models would work with other sources of uncertainty, the uncertainty associated with mapping landcover was incorporated into the model. After converting the landcover fuzzy accuracy assessment values to probabilities and re-coding the landcover map to a landcover accuracy probability surface (Figure 14), the posterior probability surface for the mountain plover was multiplied (pixel by pixel) with this landcover accuracy probability surface. The result was that most of the probability values declined due to the increased uncertainty added by the inaccuracies in the landcover classification (Figures 21 and 22). This was expected because multiplying probabilities can only reduce the resulting probability value, except that absolute certainties of habitat suitability multiplied by absolute accurate

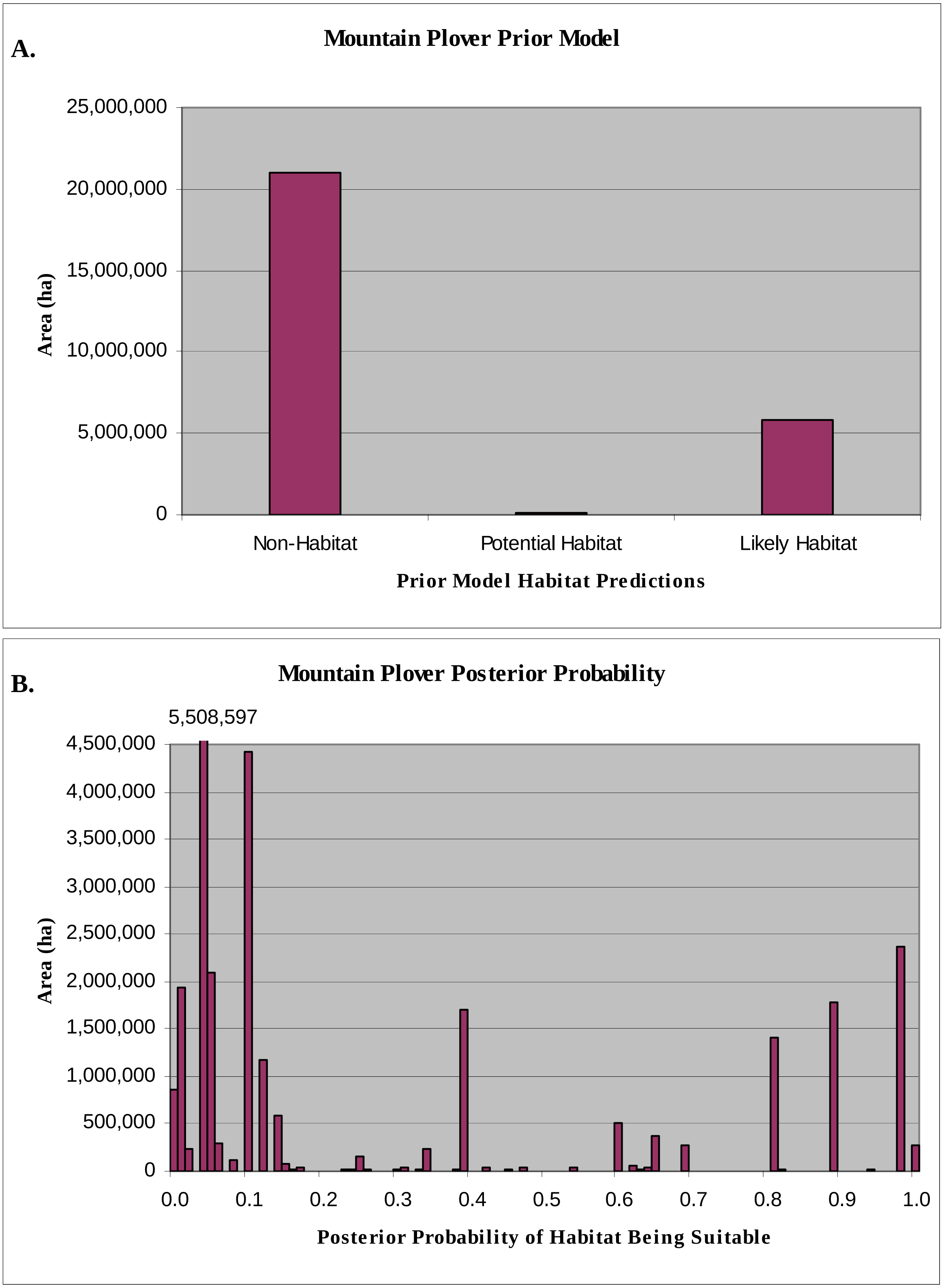
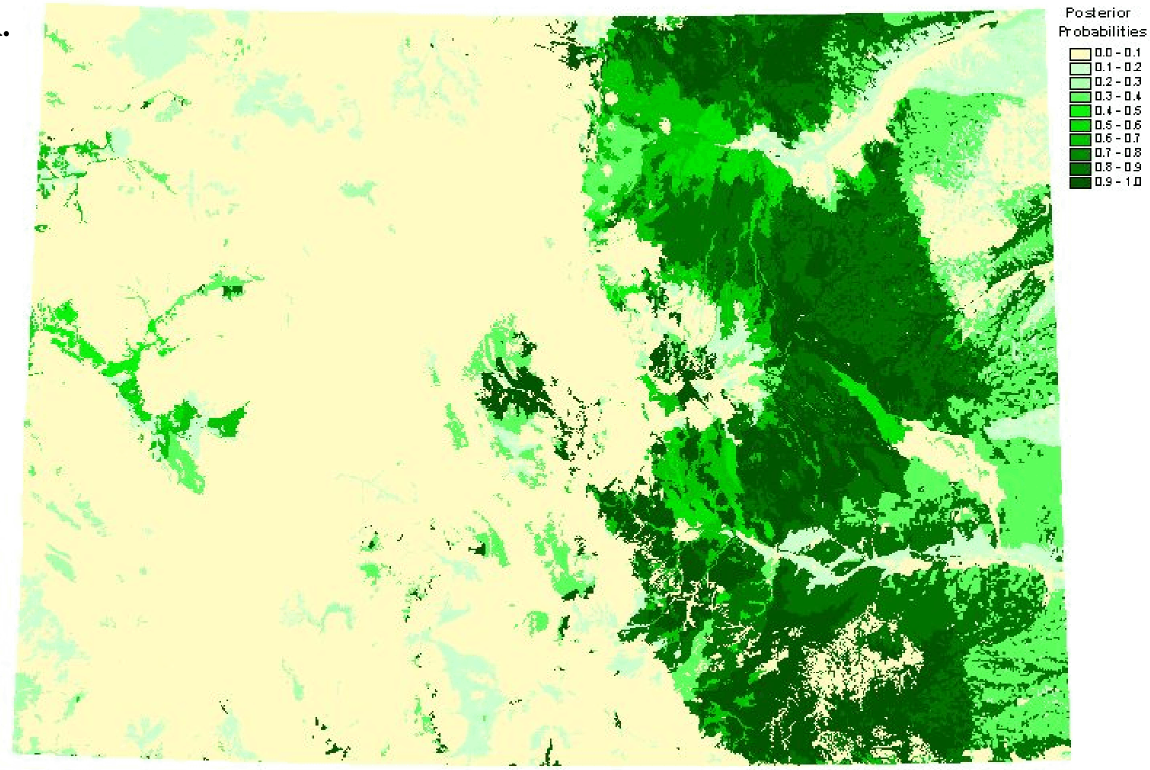


Figure 20. Histograms of Prior and Posterior Mountain Plover Models. A comparison of the area in each category of the prior habitat model (A) and the area of each probability in the posterior probability surface (B).

A.



B.

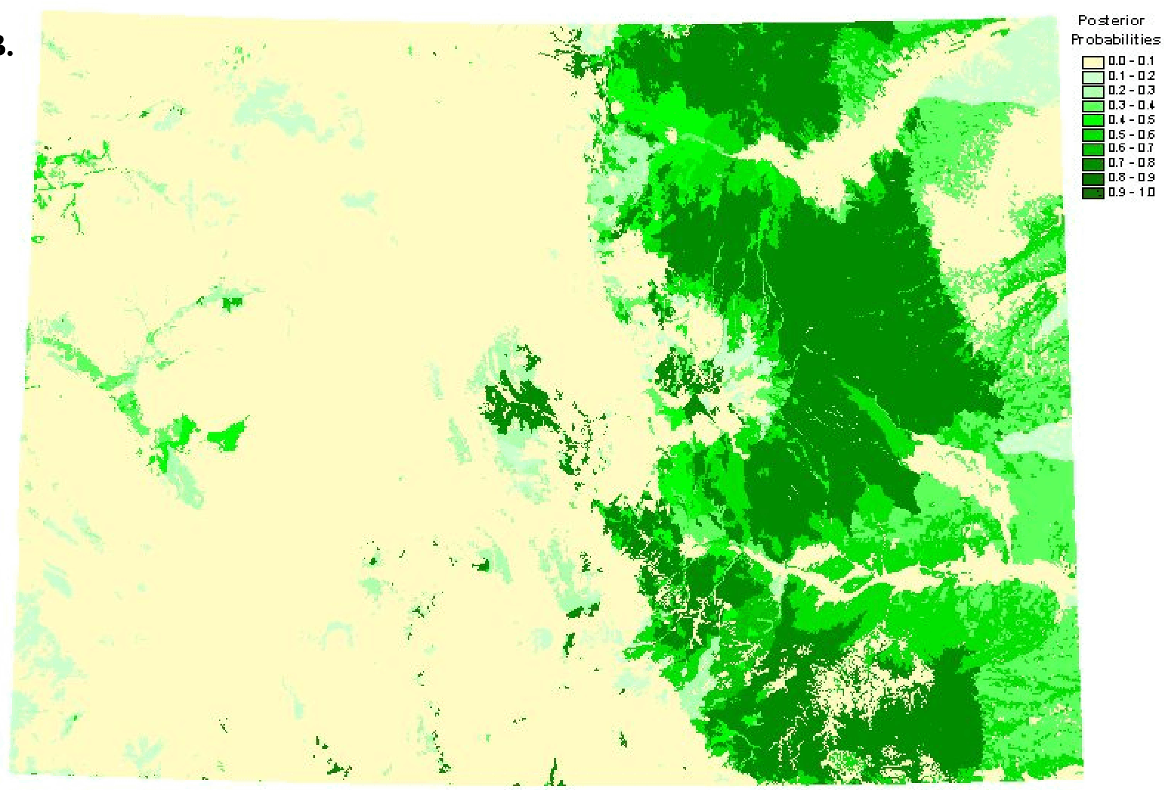
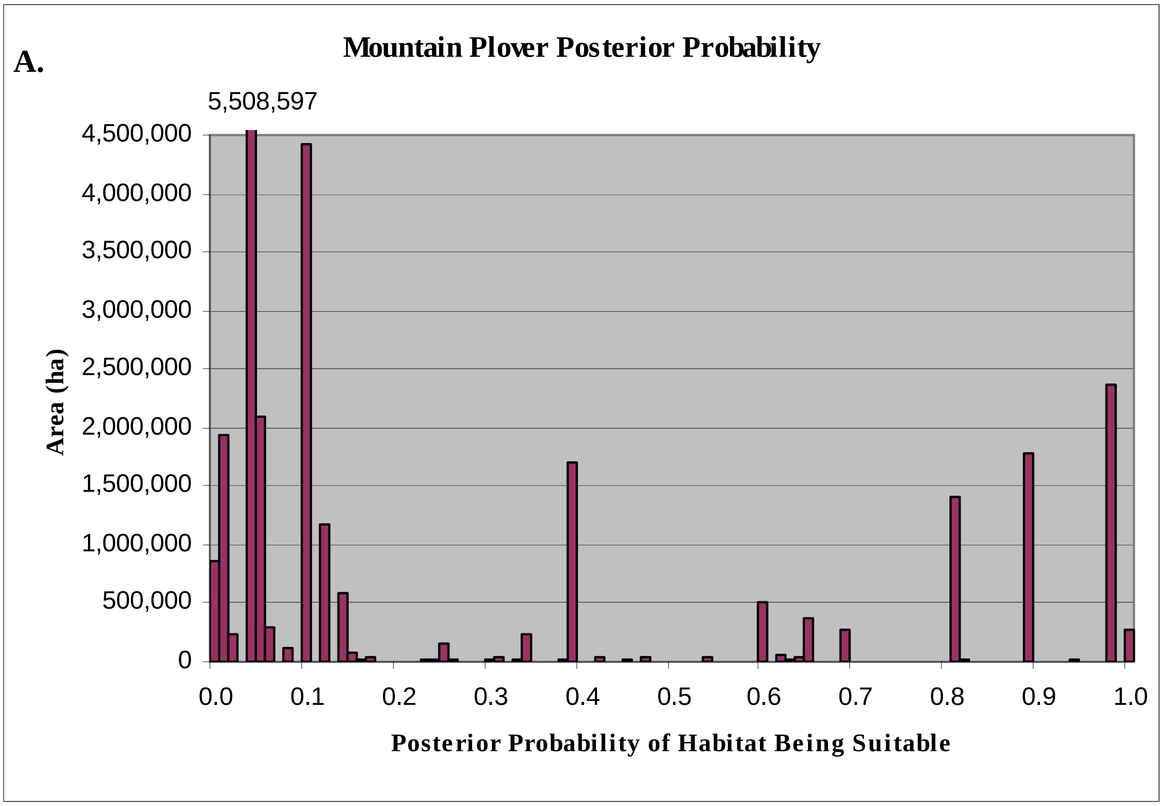


Figure 21. Posterior Probability With and Without Landcover Uncertainty for the Mountain Plover. A comparison of the mountain plover posterior probability without (A) and with (B) the uncertainty contributed by the accuracy of the landcover layer.



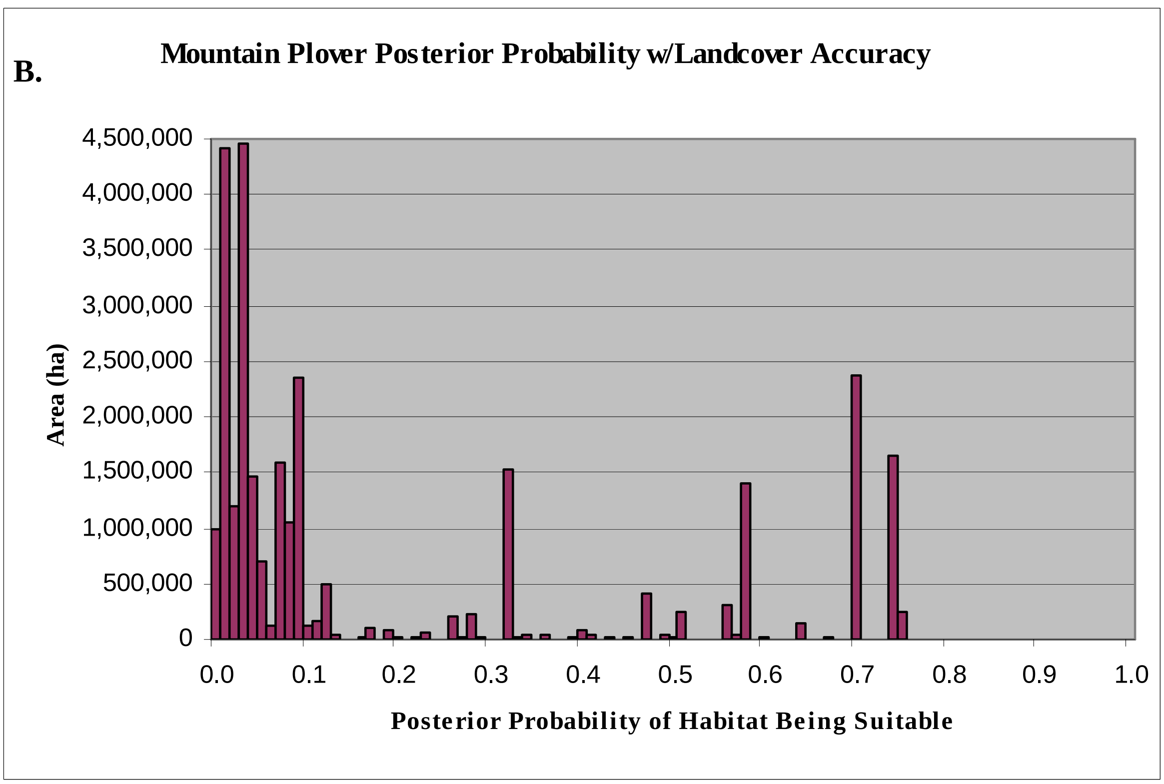


Figure 22. Histograms of Mountain Plover Models With and Without Landcover Uncertainty. A comparison of the area of each probability in the posterior probability surface without landcover uncertainty (A) and with landcover uncertainty (B).

landcover classes (probabilities of 1) would not change the resulting probability of 1, absolute certainty. Otherwise, inaccuracies in the landcover classification increase the uncertainty of the predictions of the habitat suitability map, moving areas with high certainty of being suitable habitat toward lower certainties (Figure 21). Some areas on the mountain plover posterior probability map that had some probability of being suitable habitat (upper left corner) went to near 0 and disappeared from the map (Figure 21).

The model derived for these analyses was based on the opinion of one species expert. To evaluate how this Bayesian modeling method would handle the inclusion of opinions from multiple experts, the opinions of 5 different experts on boreal toad habitat were collected.

The boreal toad experts indicated that proximity to water was an important habitat characteristic for this species, so a section was added onto the habitat review tool to collect these data. The original GAP model had buffered riparian areas as included habitats, but it did not have a specific proximity to water attribute. With the Bayesian method, adding addition information layers was not a problem.

Individual posterior probability surfaces were calculated from the habitat association probability surfaces derived from each expert's opinions (Figure 23). Two different ways were considered for combining the individual reviews into one single posterior probability surface. One method was to perform the Bayesian calculation on the average of the probability data layers from all the reviewers (5 experts x 4 habitat elements = 20 data layers) to create one combined posterior probability surface. This method has the effect of giving the prior probability surface equal weight as the average of all the expert opinion probability layers. Another method was to complete the Bayesian calculation on one expert's opinions to produce a posterior probability surface, then use that posterior probability surface as the prior probability surface in the Bayesian calculations with the next expert's opinions, and so on, calculating posterior probability surfaces using the previous posterior probability surfaces as the priors for the next iteration. This method has the effect of lessening the influence of the original prior model on the final posterior probability surface each time a new calculation is done. A comparison of the effects that these two different methods have on the final model are displayed in Figure 24. The decision as to which one of these methods is appropriate may be based upon how confident one is of the credibility of the prior model.

A comparison of the results of the first method with the prior model are shown in Figure 25. In this case, calculating the posterior probability surface for the boreal toad did not substantially change the distribution of the areas associated a gradient of habitat types from non-habitat to suitable habitat (See the histograms in Figure 26). The calculation did reveal the uncertainty inherent in the habitat associations and tended to reduce the certainty of the predictions of suitable habitat in the prior model (Table 5).

Table 5. Percentage of area in each category of the boreal toad prior habitat model and probabilities in the posterior probability surface.

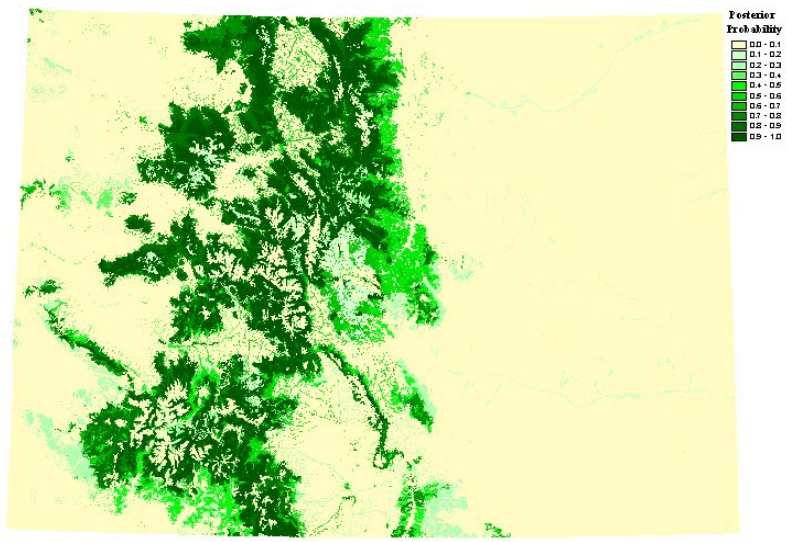
Prior Habitat Model		Posterior Probability Surface	
Non-habitat	75.1%	Probability of being suitable < 0.3	75.1%
Potential Habitat	3.2%	Probability of being suitable 0.3-0.7	7.9%
Likely habitat	21.7%	Probability of being suitable > 0.7	16.9%

The posterior probability surface resulting from the averaged expert opinions was also multiplied by the landcover accuracy probability surface to portray overall uncertainty in the boreal toad habitat suitability model (Figure 27). Again, this had the effect of generally lowering the probability of predictions of suitable habitat (see histograms in Figure 28). The magnitude of the effect for any particular area was dependent upon the classification accuracy for the landcover type in that area.

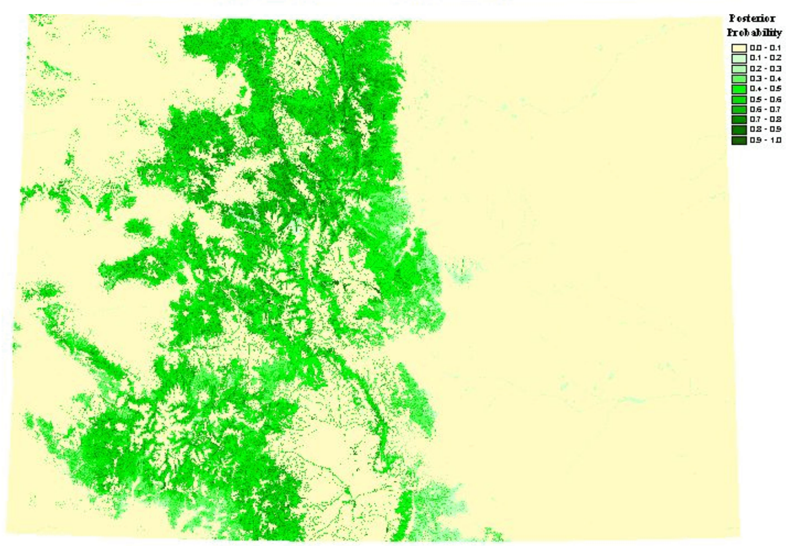
A.


Posterior Probability
0.0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0

B.


Posterior Probability
0.0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0

C.


Posterior Probability
0.0 - 0.1
0.1 - 0.2
0.2 - 0.3
0.3 - 0.4
0.4 - 0.5
0.5 - 0.6
0.6 - 0.7
0.7 - 0.8
0.8 - 0.9
0.9 - 1.0

D.

E.

F.

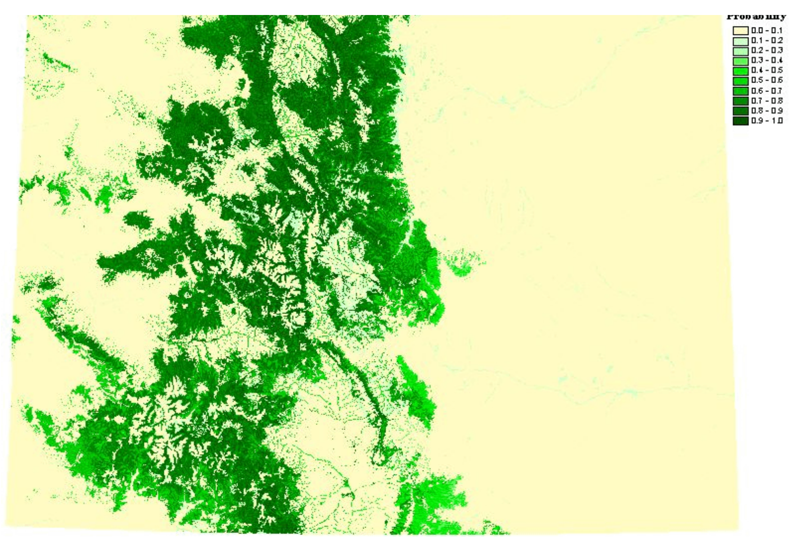


Figure 23. Individual and Combined Posterior Probabilities for the Boreal Toad. Posterior probability surfaces derived from opinions of 5 experts (A-E) and the posterior probability surface derived via Bayes' Theorem from the averaged opinions (F).

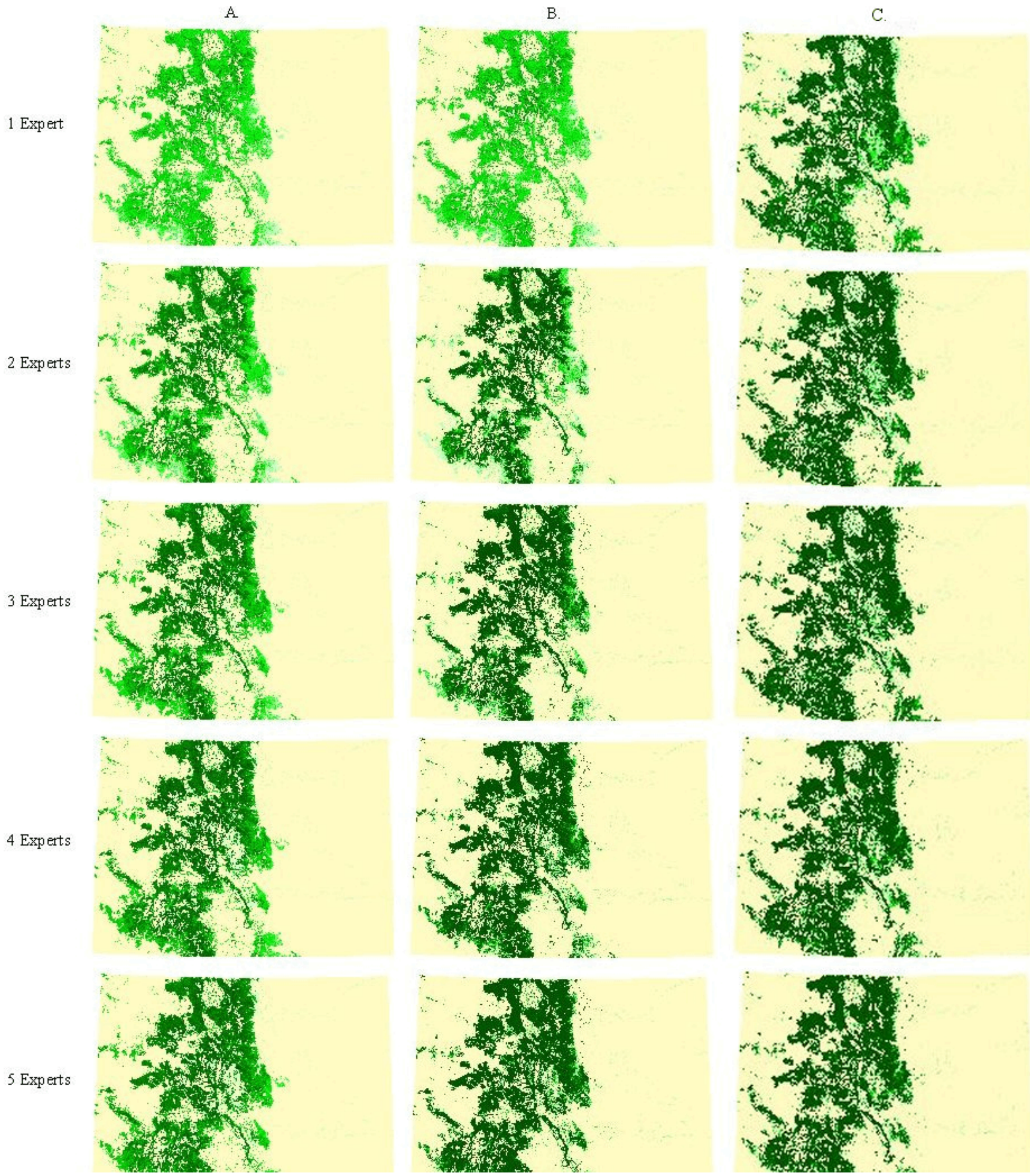


Figure 24. Averaged Expert Opinions vs Iterative Bayes' Calculations. Posterior probability surfaces with expert opinions averaged together and then combined with the prior probability surface using Bayes' Theorem (A) compared to using each posterior probability surface as the prior in iterative Bayes' calculations (B) and then reversing the order of posterior probabilities entered into the iterative calculations (C).

A.

B.

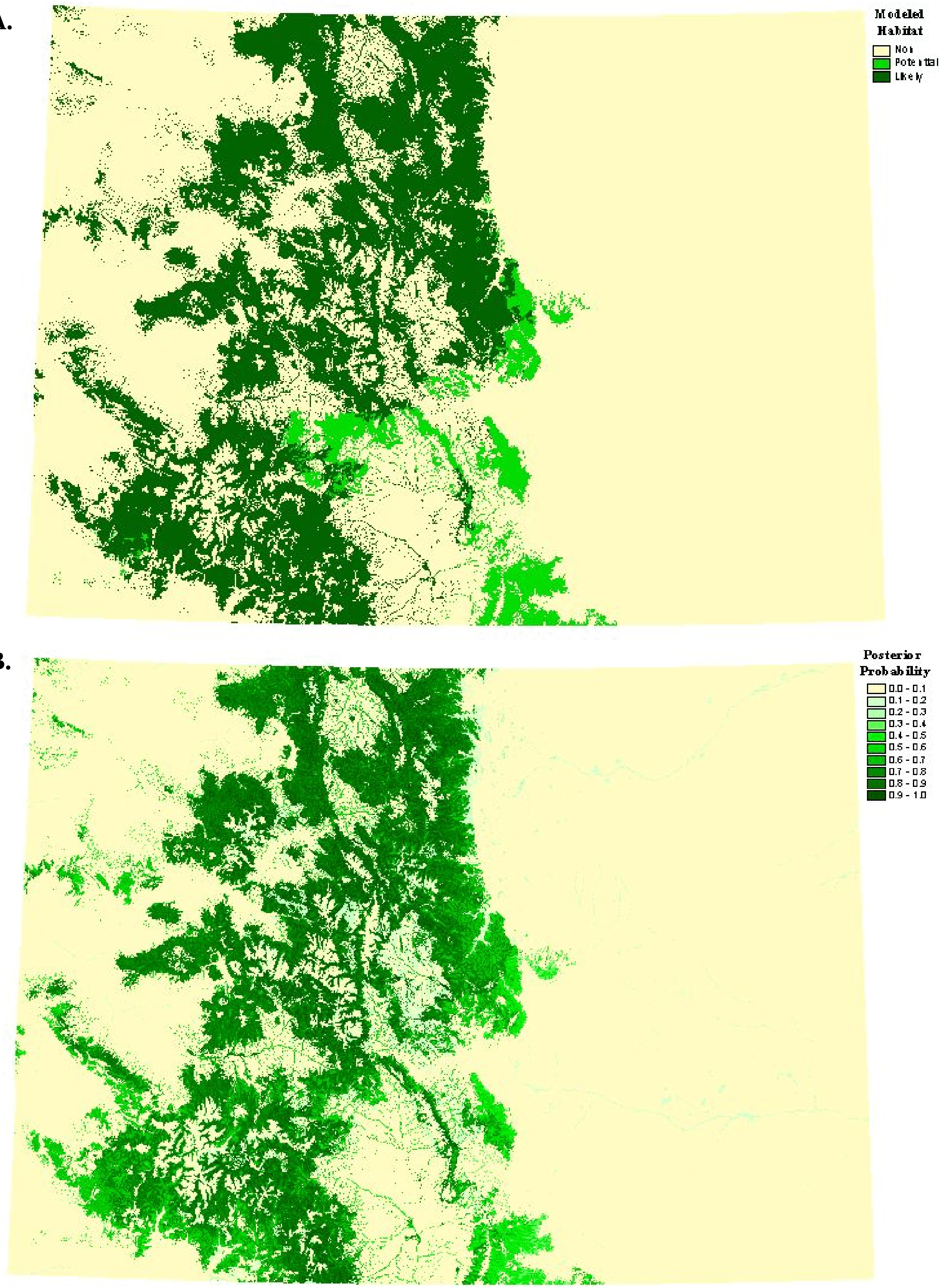


Figure 25. Prior and Posterior Probability Surfaces for the Boreal Toad. A comparison of the boreal toad prior model (A) and posterior probability surface (B). The latter was derived by averaging the expert opinion probability surfaces together and using the averaged layer in the Bayes' calculation of posterior probability.

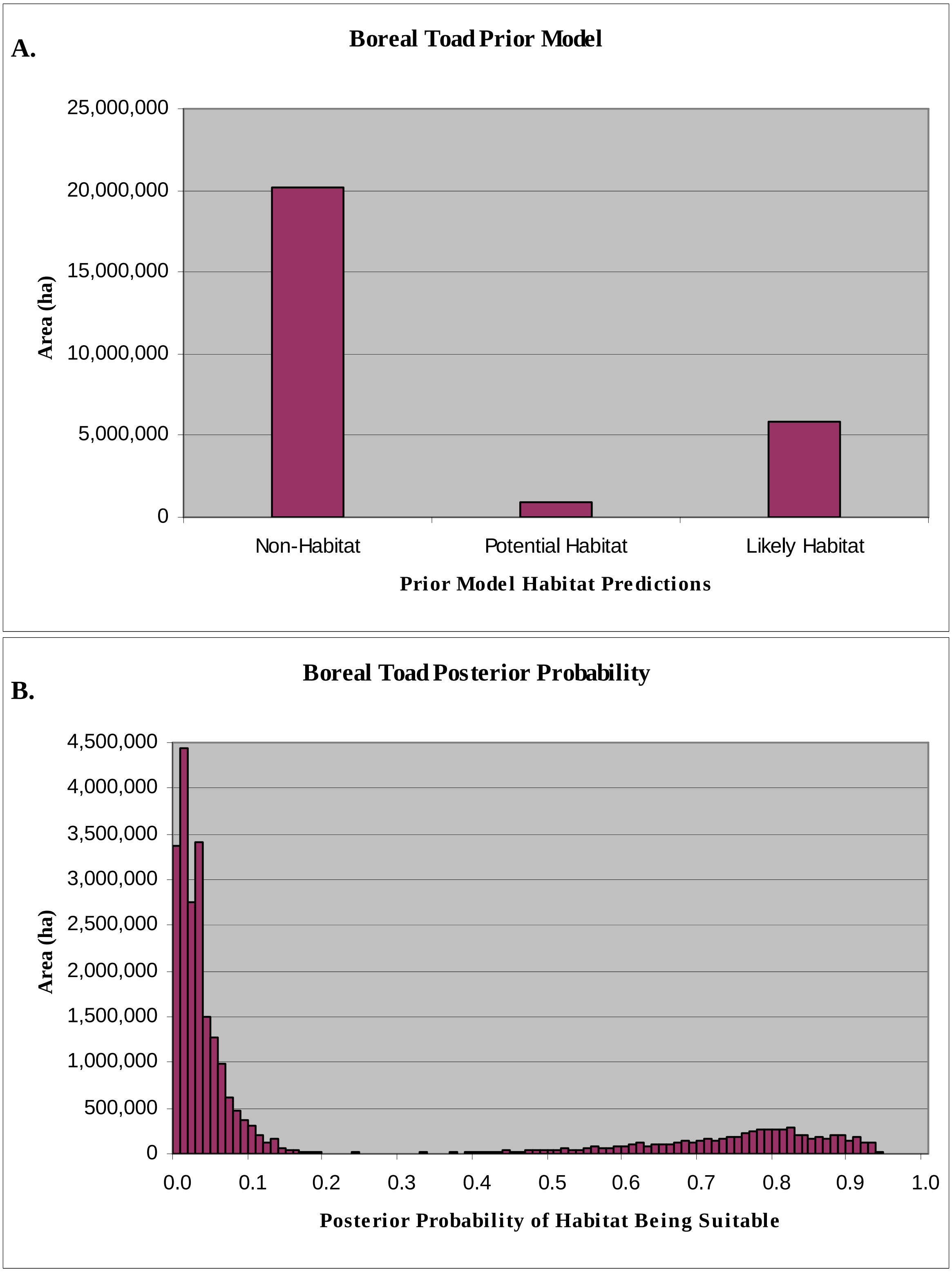
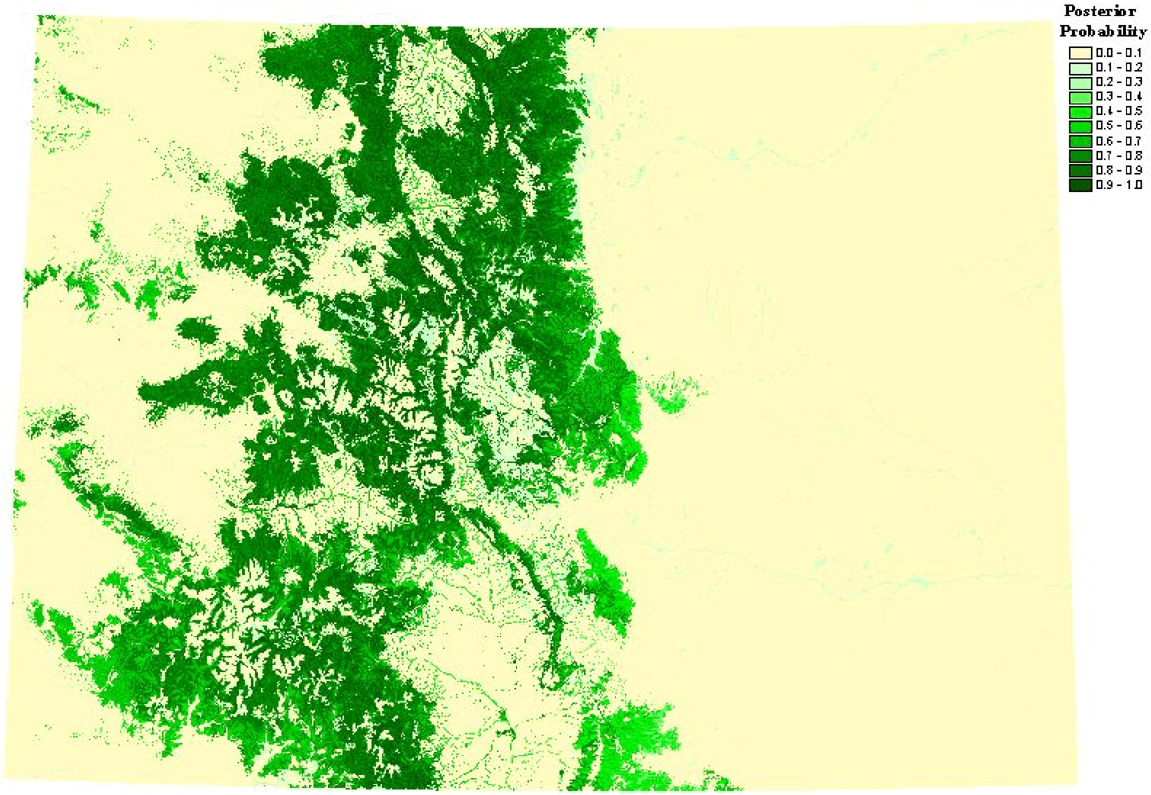


Figure 26. Histograms of Prior and Posterior Boreal Toad Models. A comparison of the area in each category of the prior habitat model (A) and the area of each probability in the posterior probability surface (B).

A.



B.

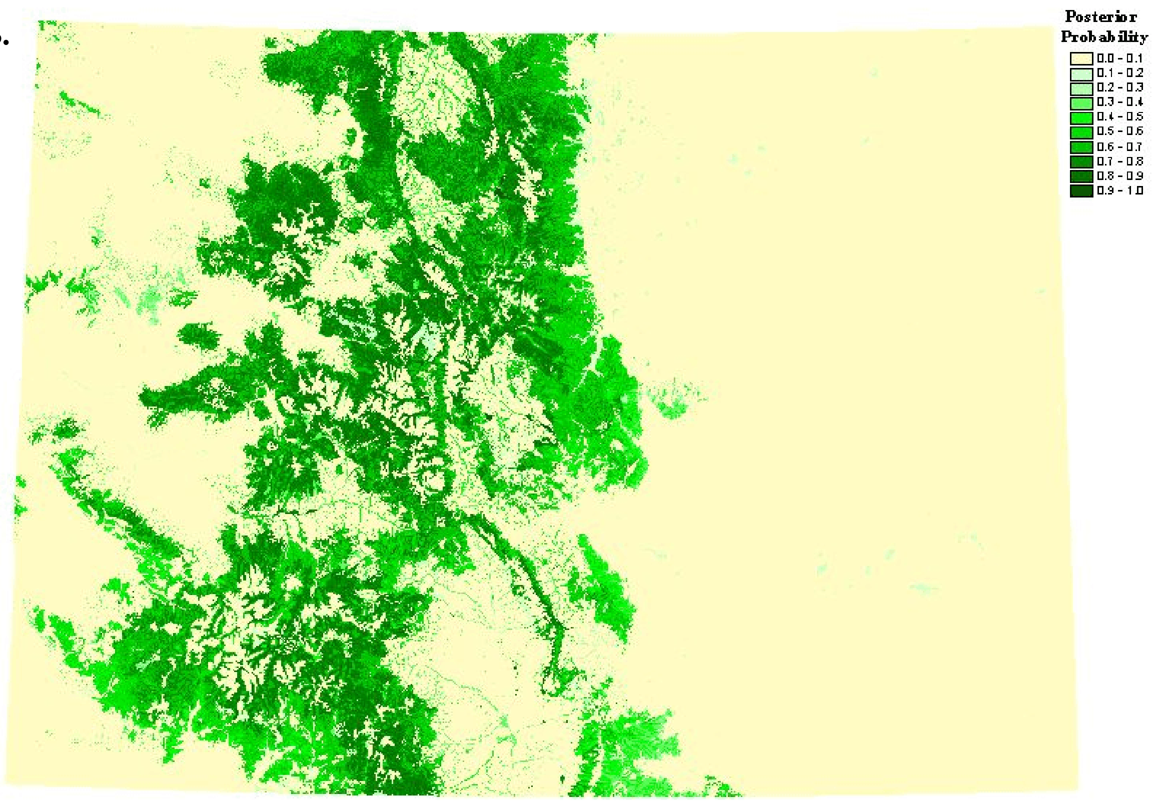


Figure 27. Posterior Probability With and Without Landcover Uncertainty for the Boreal Toad. A comparison of the boreal toad posterior probability without (A) and with (B) the uncertainty contributed by the accuracy of the landcover layer.

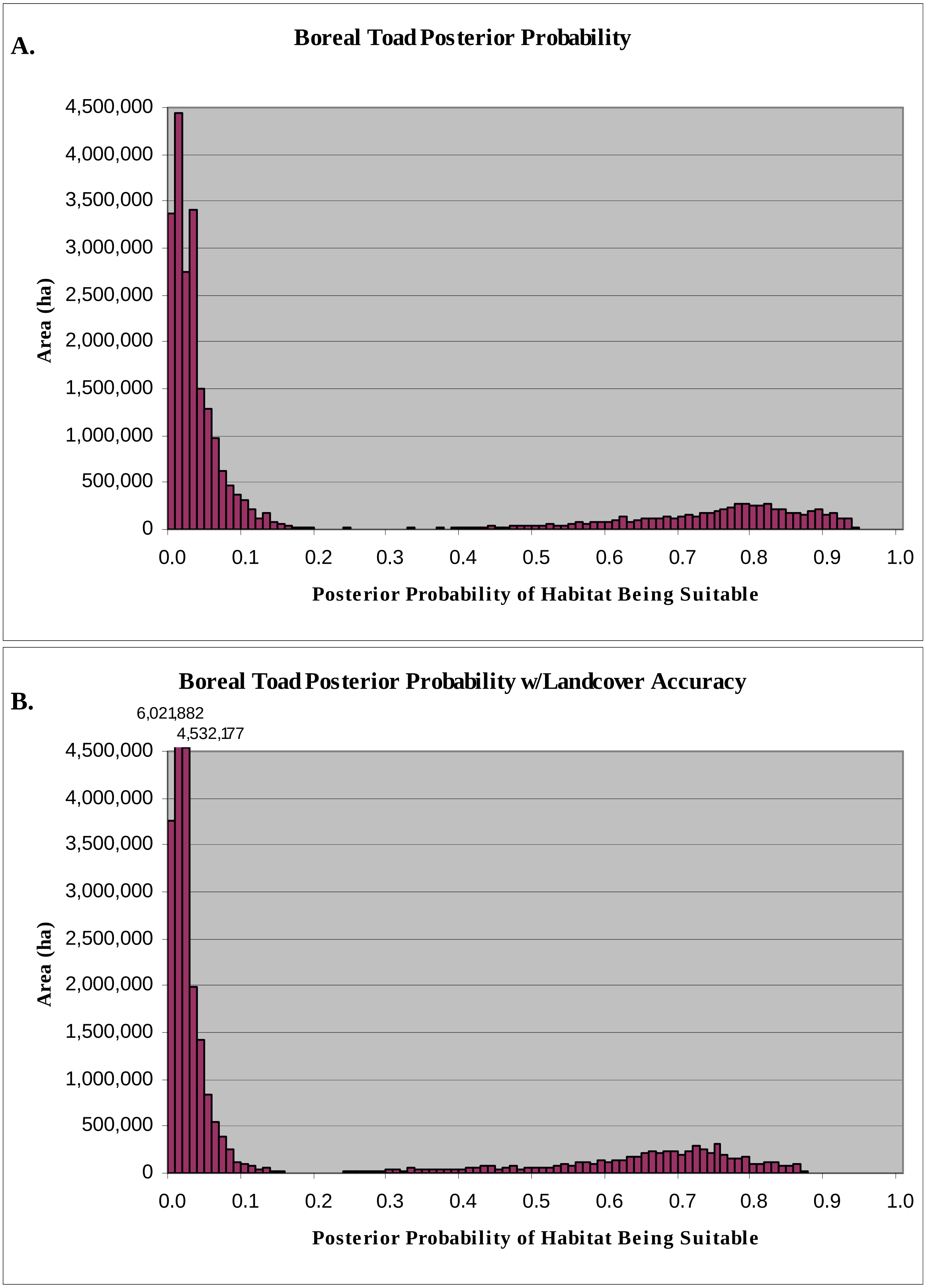


Figure 28. Histograms of Boreal Toad Models With and Without Landcover Uncertainty. A comparison of the area of each probability in the posterior probability surface without landcover uncertainty (A) and with landcover uncertainty (B).

The final test of the proposed Bayesian method was to ascertain how the models would handle the addition of landscape context. A posterior probability surface was derived for the lynx using a species expert's opinions and the prior Colorado GAP model for the lynx (Figure 29). Similar to the results of the mountain plover model, many areas that were classified as unsuitable habitat in the prior model are shown to have a probability of being suitable in the lynx posterior probability surface (Figure 18). Again, these areas would have been excluded from consideration in lynx management and conservation plans using the existing GAP habitat model. The change in classification of areas tended to be from areas being considered non-suitable habitat to areas having some to high probability of being suitable (Table 6).

Table 6. Percentage of area in each category of the lynx prior habitat model and probabilities in the posterior probability surface.

Prior Habitat Model		Posterior Probability Surface	
Non-habitat	83.7%	Probability of being suitable < 0.3	78.6%
Potential Habitat	0.2%	Probability of being suitable 0.3-0.7	4.5%
Likely habitat	16.1%	Probability of being suitable > 0.7	16.9%

Histograms of the area in prior habitat categories and of the area with different posterior probabilities show the distribution of areas across these categories (Figure 30). The graphs show the increase in the middle range of probabilities.

The posterior probability surface was re-coded with hypothetical probabilities of the suitability of each non-contiguous habitat patch based upon the size of the patch (Table 2). This probability surface (Figure 18) was then entered into the Bayesian calculation of the posterior probability surface. This had a small effect of decreasing the probability of smaller patches and increasing the probability of larger patches of being suitable habitat

(Figures 31and 32). Some of the smaller patches in the functional landscape (Theobald and Hobbs 2002) may be important as “stepping stones” between larger habitat patches, whereas smaller patches that are isolated from other habitat patches may be less important. This method can be used to incorporate other important landscape context configurations such as this by including them as probabilities of contributing to (or constraining) suitable habitat. Patch isolation and size could be combined together into a probability surface and brought into the model.

This method allows these types of landscape metrics to be brought into habitat model as probabilities. This is in contrast to making a priori decisions to delete potentially suitable habitat that does not meet predetermined criteria. This modeling method preserves the assumptions that go into building the model and reflects these in the resulting depiction of uncertainty.

Lastly, the landcover accuracy probability surface was combined with the patch size posterior probability surface by multiplying the grids together. As expected, the probability of habitat being suitable went down in proportion to the inaccuracy of the classification of the landcover types (Figures 33 and 34).

Assuming that the accuracy of each habitat association dataset could be quantified, that all relevant habitat associations could be assigned levels of certainty by species experts, and that multiple species experts could be consulted to ameliorate the opinions of any one expert, then this method has the potential to depict the overall state of knowledge about the distribution of suitable habitat and spatially reflect the uncertainty associated with the predictions.

A.

B.

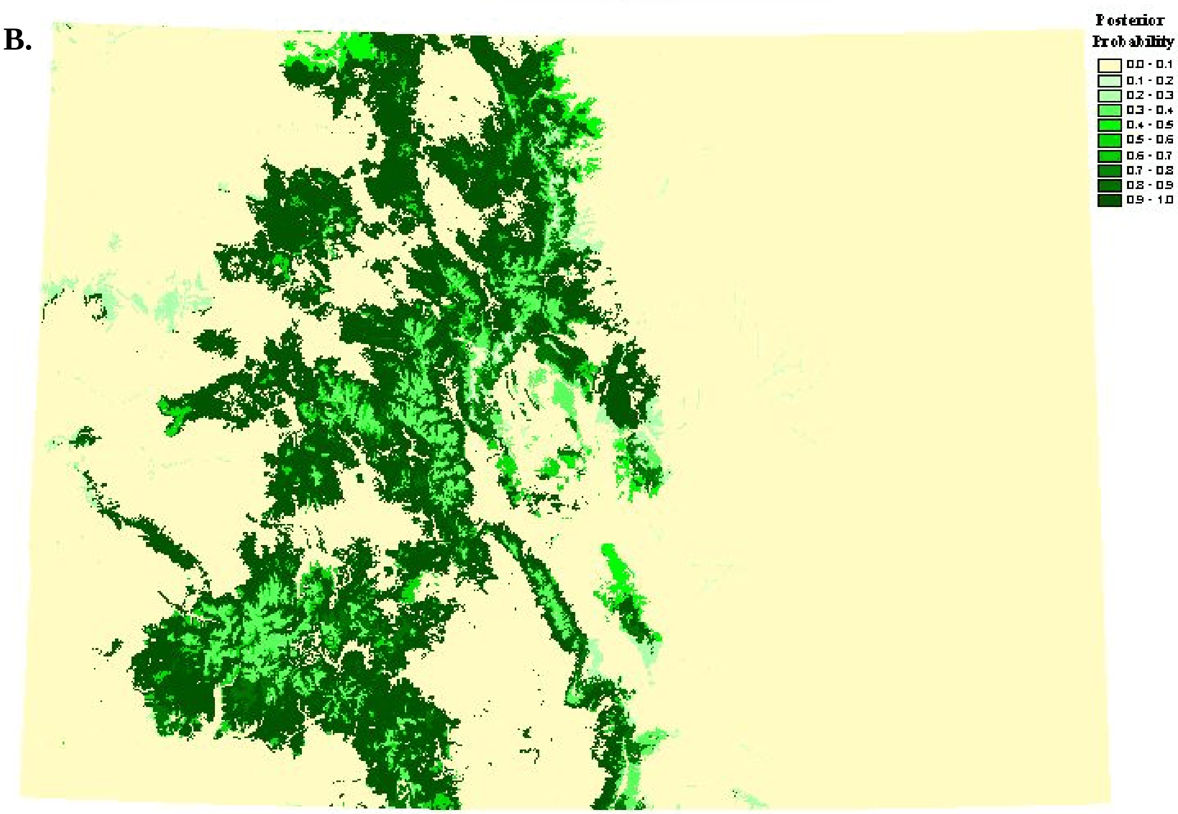


Figure 29. Prior and Posterior Probability Surfaces for the Lynx. A comparison of the lynx prior model (A) and posterior probability surface (B).

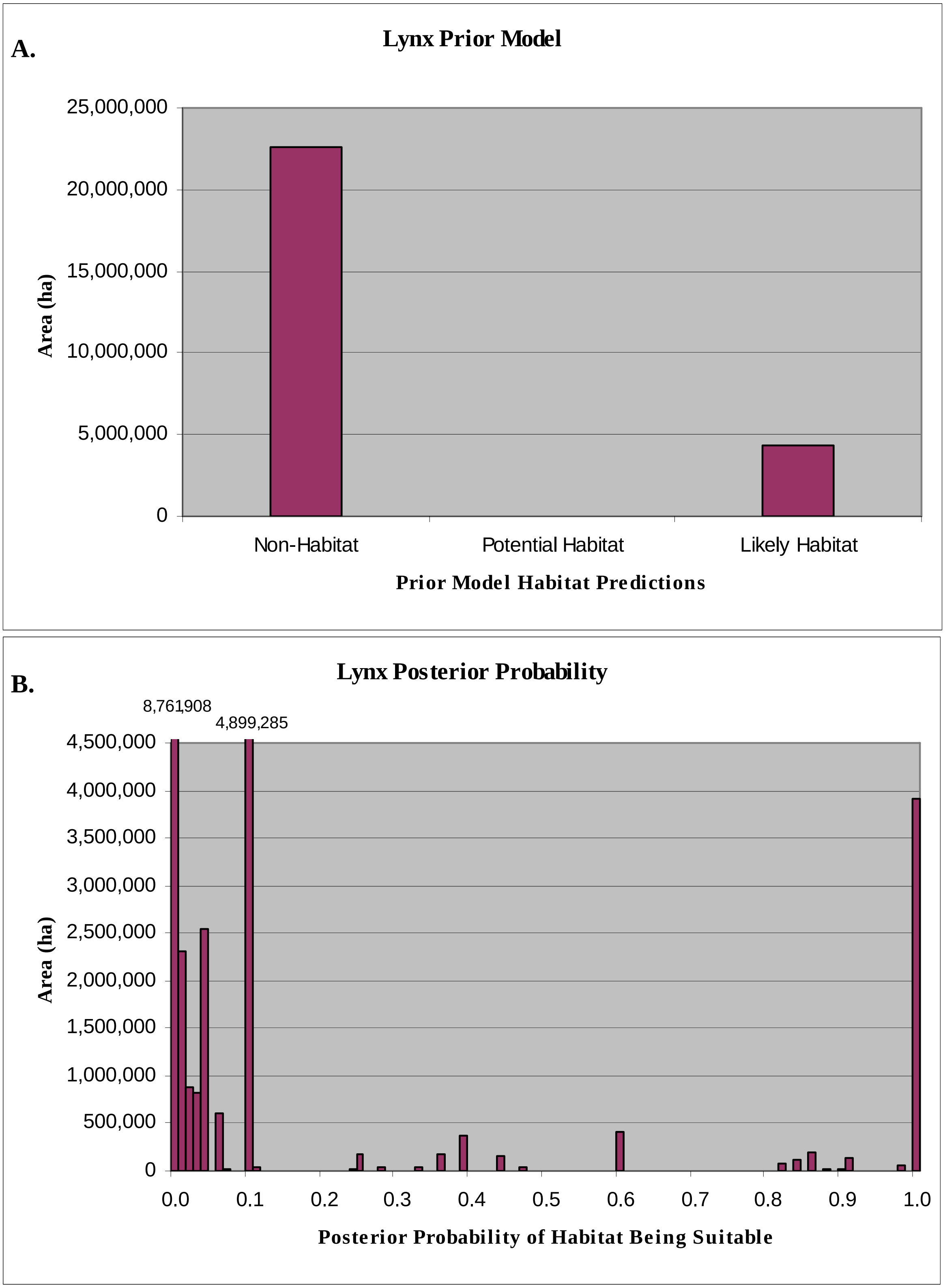
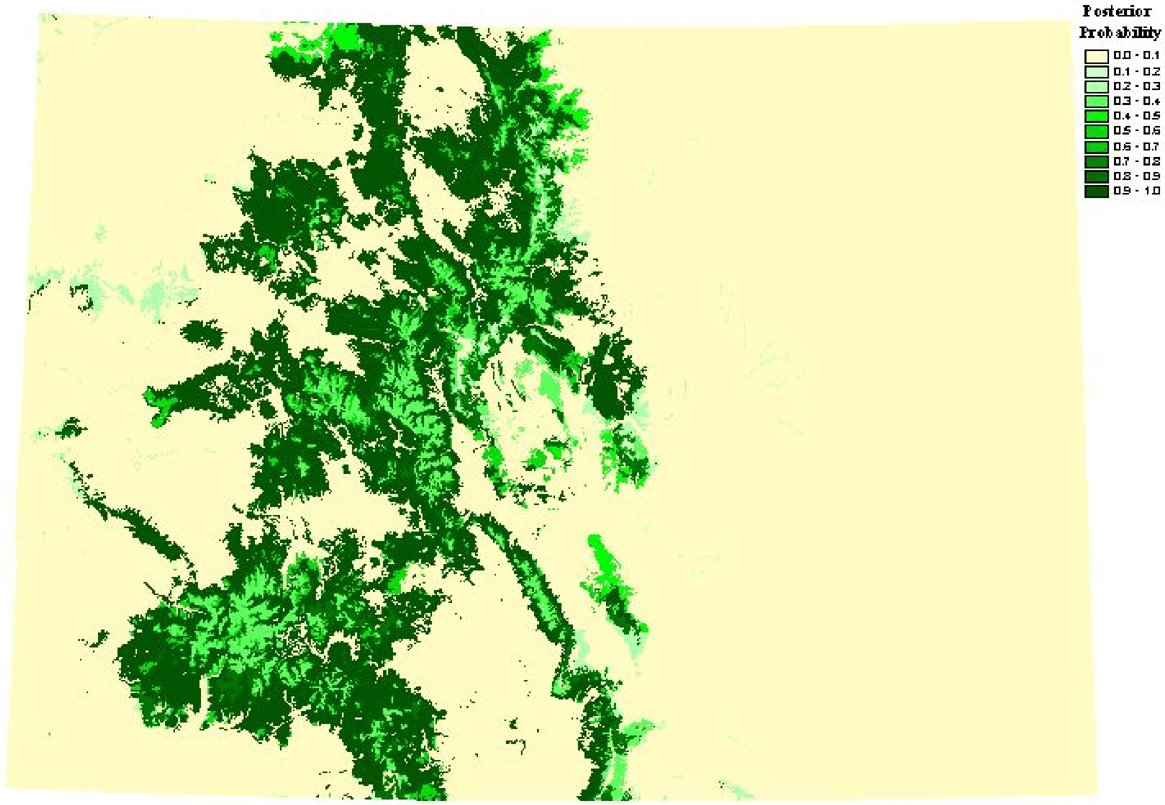


Figure 30. Histograms of Prior and Posterior Lynx Models. A comparison of the area in each category of the prior habitat model (A) and the area of each probability in the posterior probability surface (B).

A.



B.

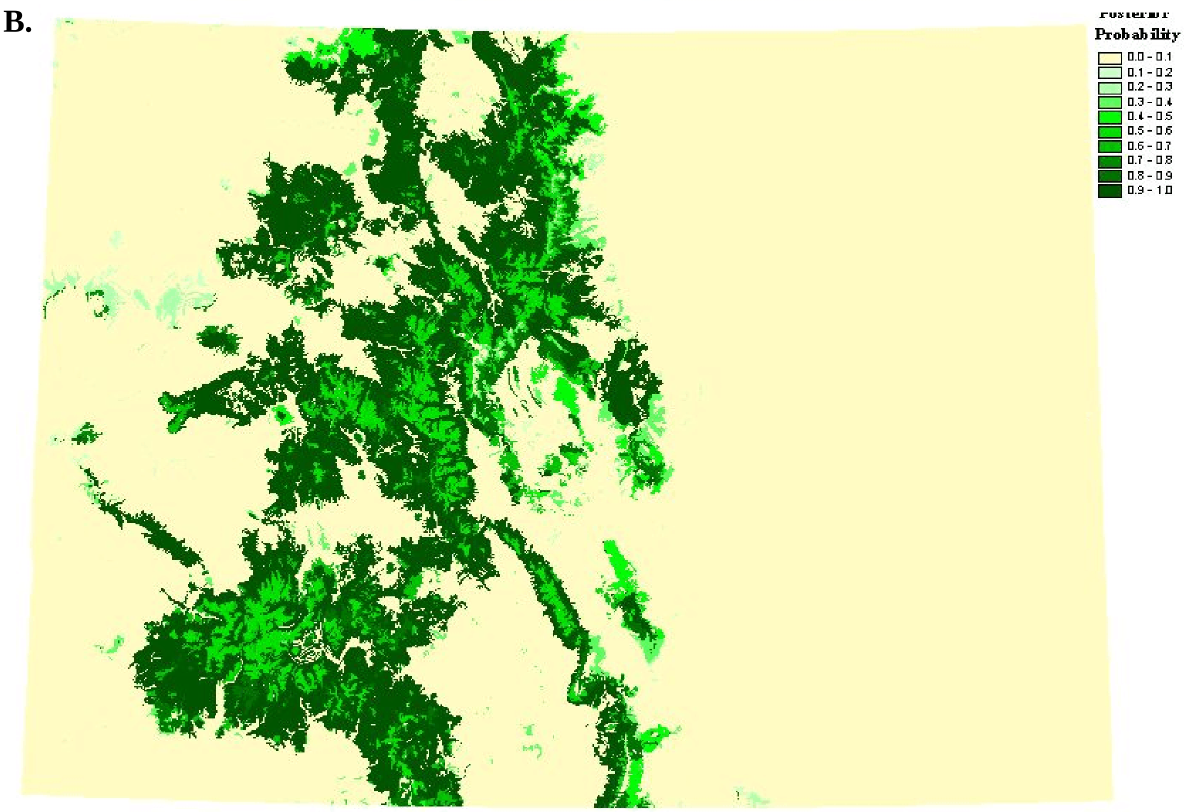
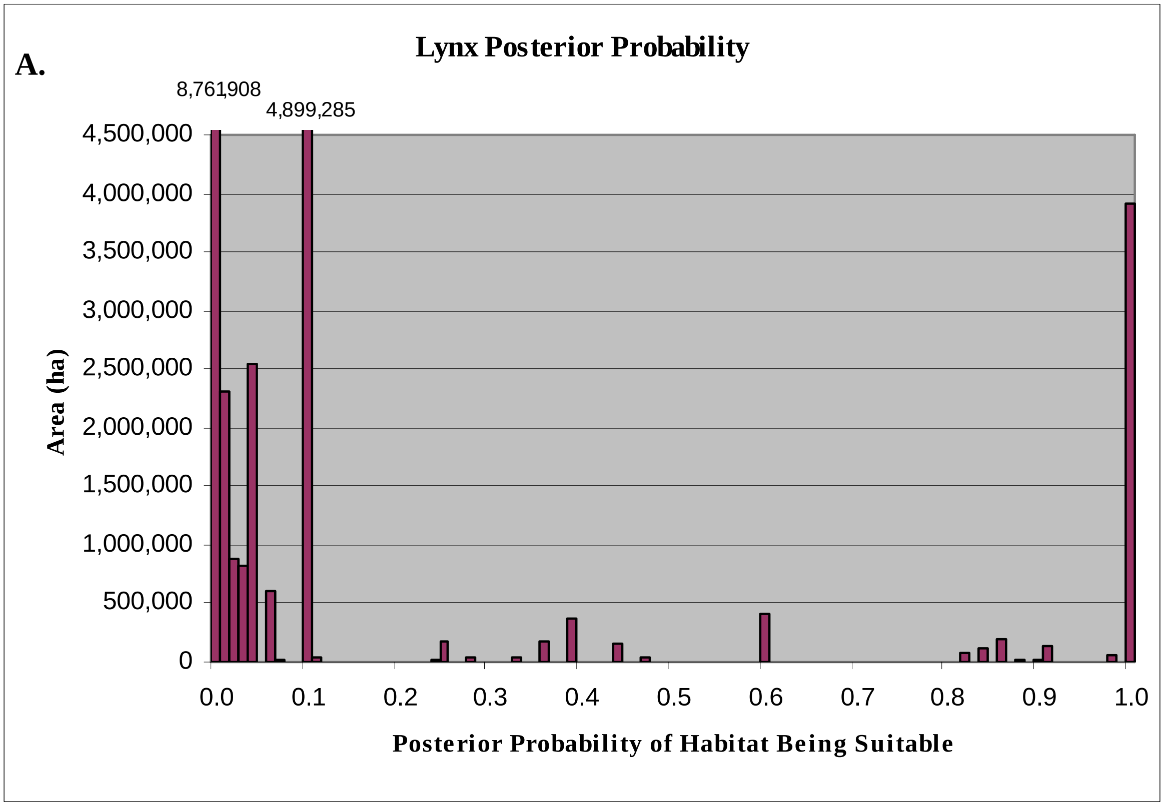


Figure 31. Posterior Probability With and Without Lynx Patch Size Probability. A comparison of the lynx posterior probability surfaces without (A) and with (B) the probabilities related to habitat patch size added into the model.



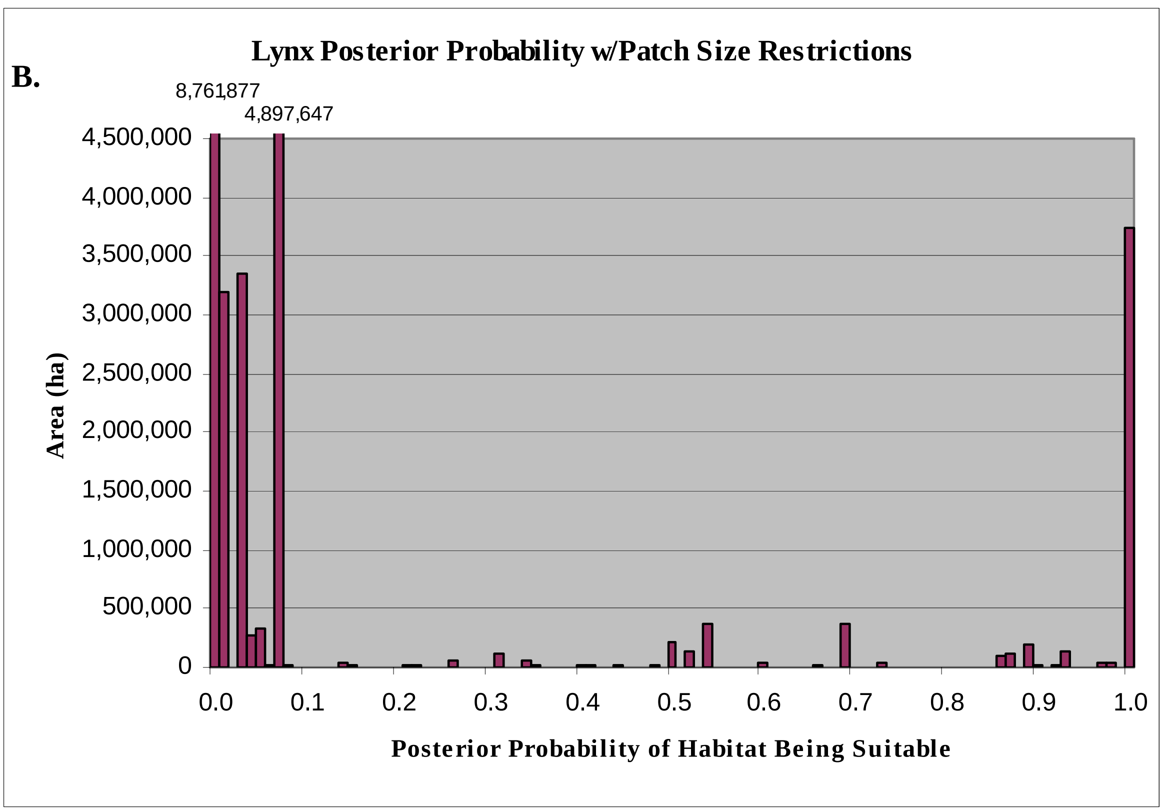
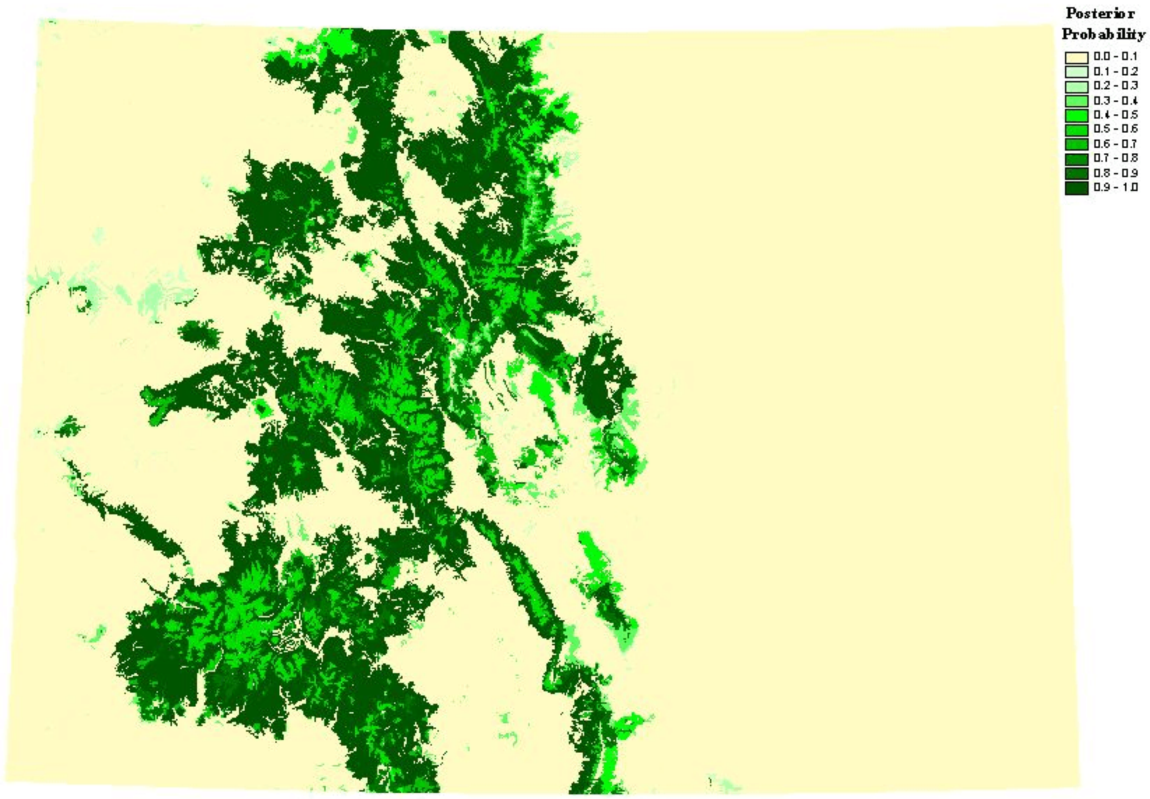


Figure 32. Histograms of Lynx Models With and Without Patch Size Probability. A comparison of the area of each probability in the posterior probability surface without patch size probability (A) and with patch size probability (B).

A.



B.

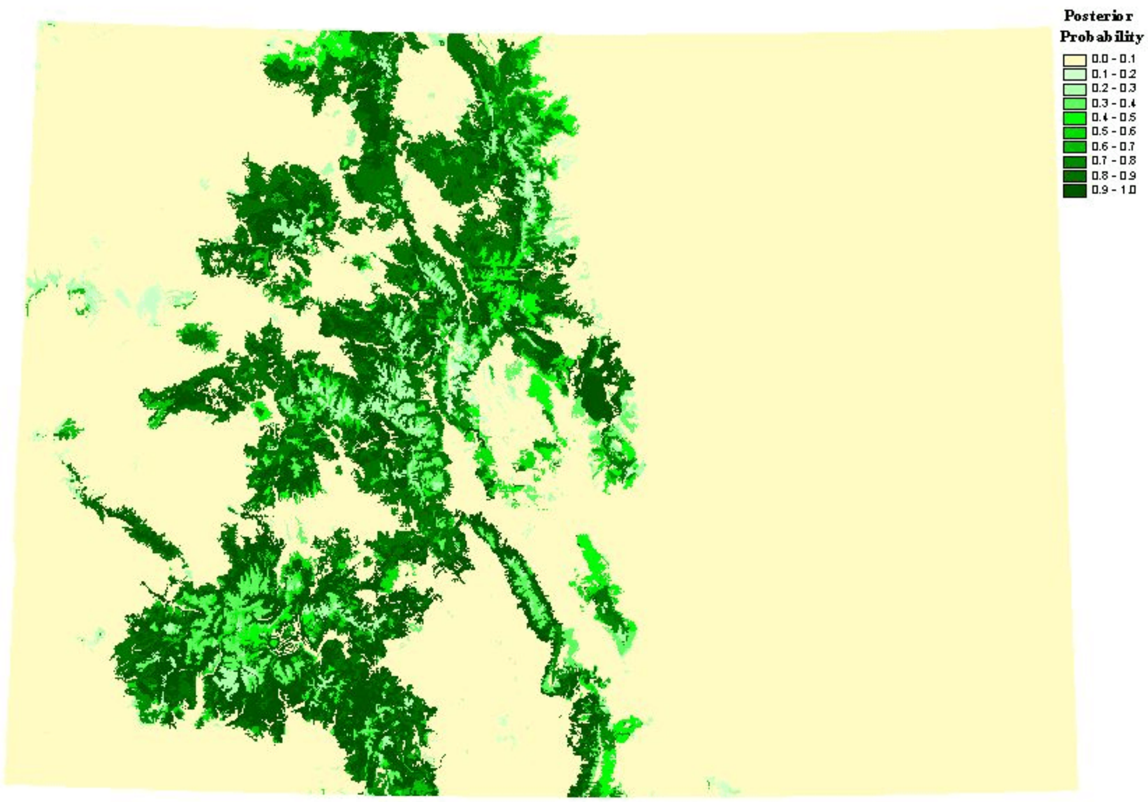


Figure 33. Lynx Patch Size Probability With and Without Landcover Accuracy. A comparison of lynx posterior probability surfaces including patch size probability without (A) and with (B) the uncertainty contributed by the accuracy of the landcover layer.

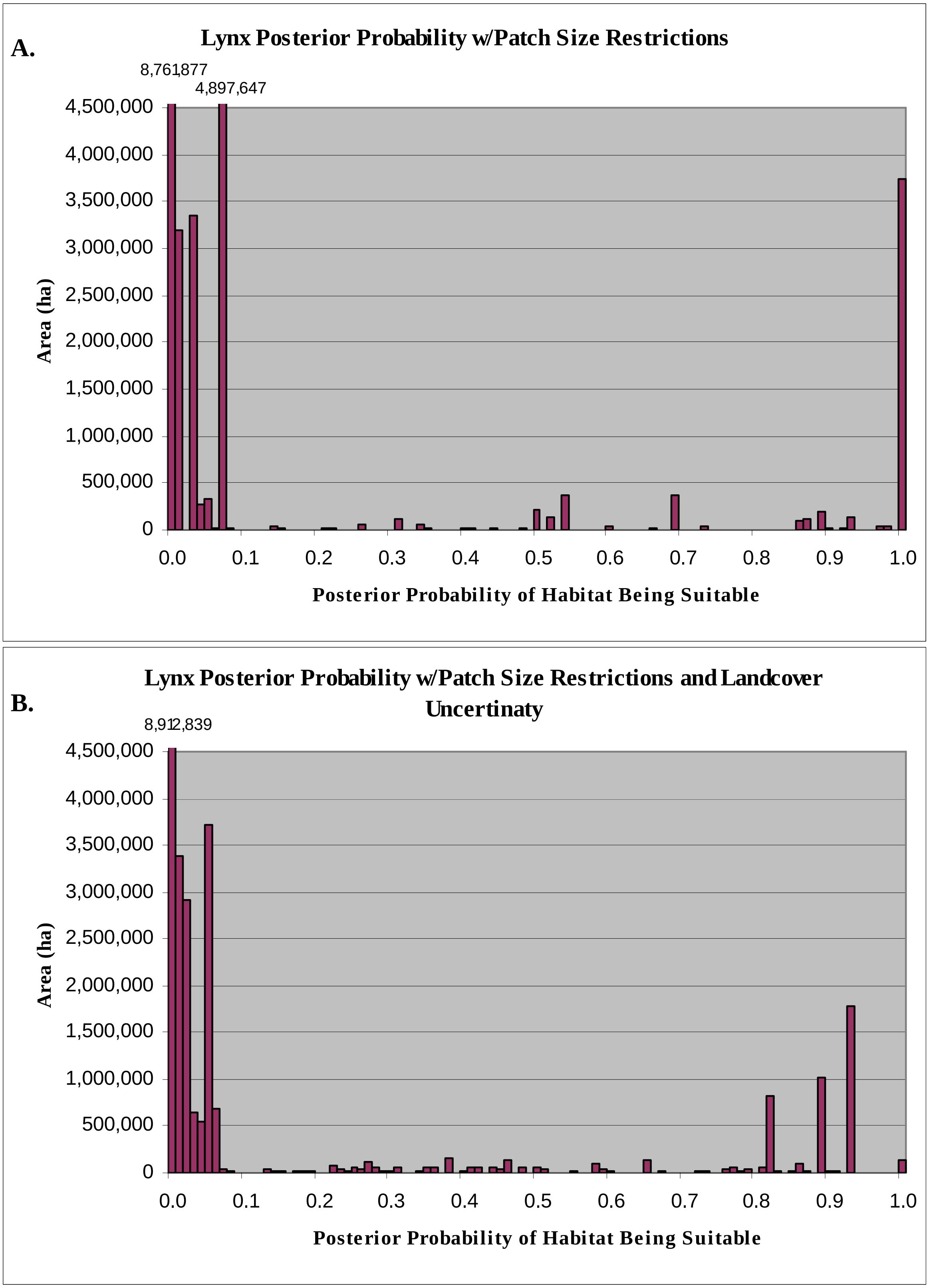
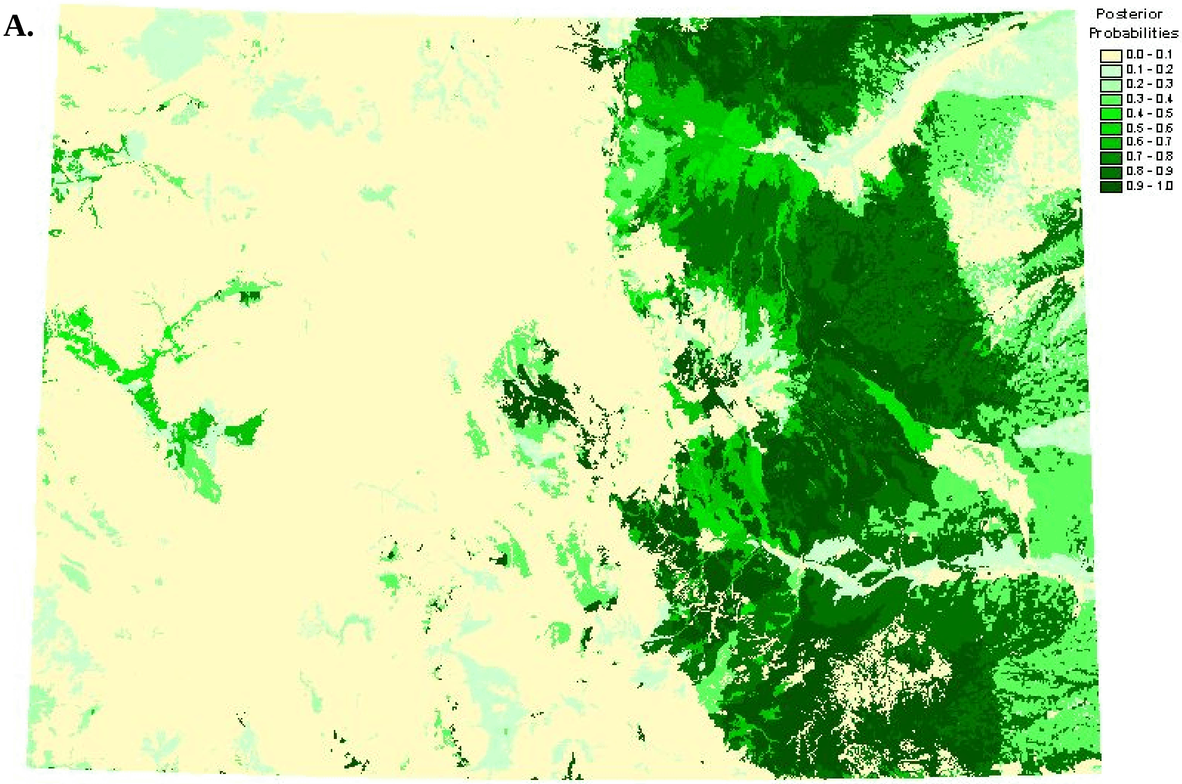


Figure 34. Histograms of Lynx Patch Size Probability With and Without Landcover Uncertainty. A comparison of the area of each probability in the posterior probability surface without landcover uncertainty (A) and with landcover uncertainty (B).

The sensitivity of these models to some of the assumptions made in designing them were tested in several ways. One decision made in designing the models was to give the landcover dataset twice the weight as the other habitat datasets (elevation and range). This was done to increase the effect of the landcover associations, which, for most species, is the main predictor of the suitability of habitat. The other habitat associations used in the models limit where suitable habitat is predicted. When comparing the mountain plover habitat model created with landcover given twice the weight of other habitat elements (Figure 35A) to the same model with all habitat elements given equal weight (Figure 35B), the effects from the geographic range dataset can clearly be seen in the latter model (see also the mountain plover range probability surface in Figure 7). The equally weighted model predicts the entire North Park watershed (top center of the map) to be suitable habitat, whereas the model giving landcover double emphasis predicts a much smaller area within the watershed to be suitable habitat. The entire geographic range of a species is not necessarily suitable habitat. Rather, suitable habitat is a subset of a species' geographic range. In these models, suitable habitat is predicted by the distribution of suitable landcover constrained by range and elevation. This was the reasoning behind the decision to increase the effects of landcover in relation to the other habitat elements in the model. This decision needs to be disclosed when describing the models.

Since these models are Bayesian, they rely upon updating prior information to make inferences. To test the effect that this prior information has on the predictions of the models, three different types of sensitivity analyses were done. In the first evaluation, an area of the boreal toad prior probability surface that was indicated to be unsuitable (0.1) in the prior model and by all species experts was changed to a probability of 0.6 (Figure 36).

A.



B.

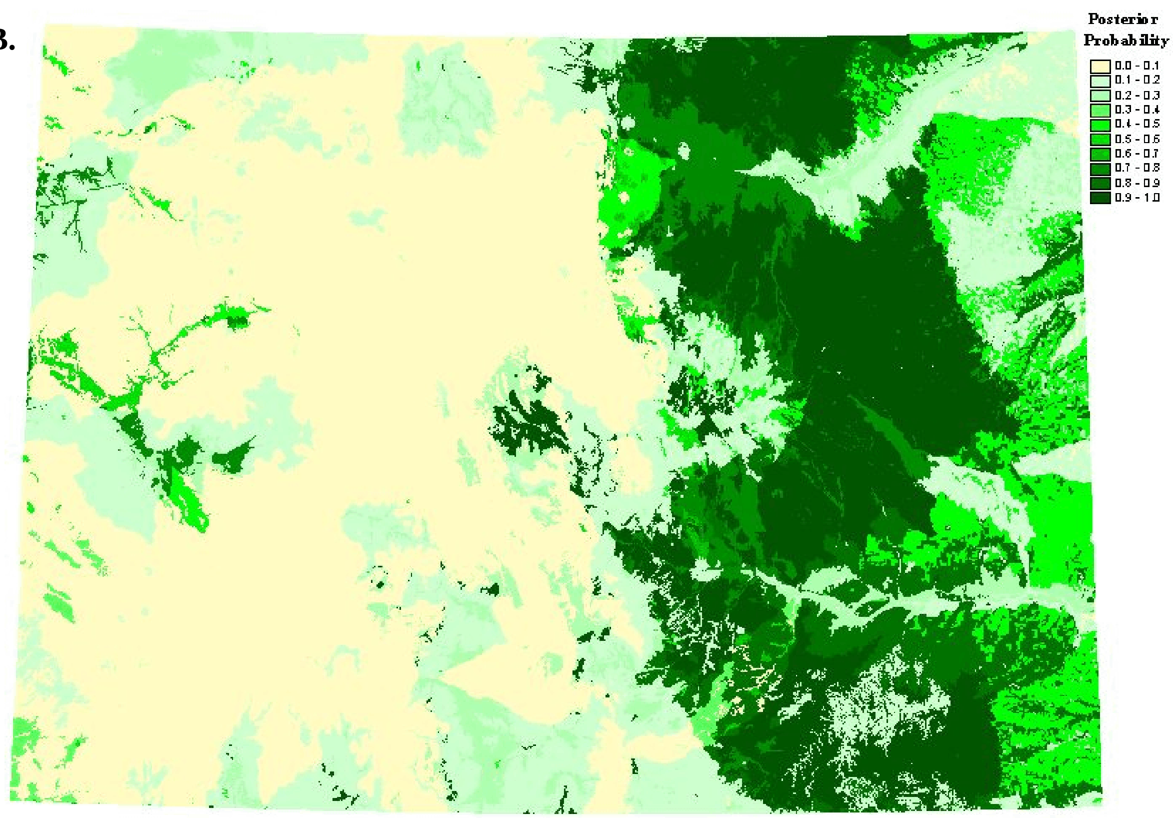


Figure 35. Sensitivity of Model to Weighting the Landcover Probability Surface. Mountain plover posterior probability with the landcover probability surface multiplied by 2 (A) and with all probability surfaces used in Bayes' calculation weighted equally (B).

0.1 to 0.6 in the prior probability surface for the boreal toad model (Figure 36). This altered probability surface was used in the Bayesian calculations of the posterior probability surface with the opinions of 1 through 5 different species experts added to the model. This was done by both methods of combining species expert opinions, by averaging them together and by iteratively calculating Bayes' Theorem. As can be seen in the results (Figure 37), the misclassified prior probabilities have an effect on the models (compare to Figure 24). The effect is less for the models in which expert opinions are incorporated iteratively (Figure 37, Column B). This makes intuitive sense, because the other method, by averaging, gives less weight to expert opinions relative to the prior probability surface. The effect of the order of the iterative calculations was also analyzed by reversing the order of the experts posterior probabilities used in the iterative Bayes' calculations (Figure 24). The order that expert posterior probabilities are entered into the iterative Bayes' calculations do not seem to have much effect after the fourth expert's results are factored in.

The influence of prior probabilities was also tested by individually altering the assignments of probabilities to prior model habitat categories, while holding the other probability values constant, and observing the effects on posterior probabilities. In this evaluation the non-habitat category (assigned probability 0.1) in the mountain plover prior model was assigned to probabilities of 0.0, 0.1, 0.3, 0.5, 0.8 and 1.0, while the other 2 habitat categories, potential and likely habitat, were held constant at 0.5 and 0.6 respectively. This was done for each habitat category in turn, altering them across the same range of values while holding the other two constant. The results shown in Figure 38, Columns A, B and C, show that altering the 0.1 prior probability had a large effect on the model, altering the 0.5 prior had almost no effect on the model, and altering the 0.6 prior

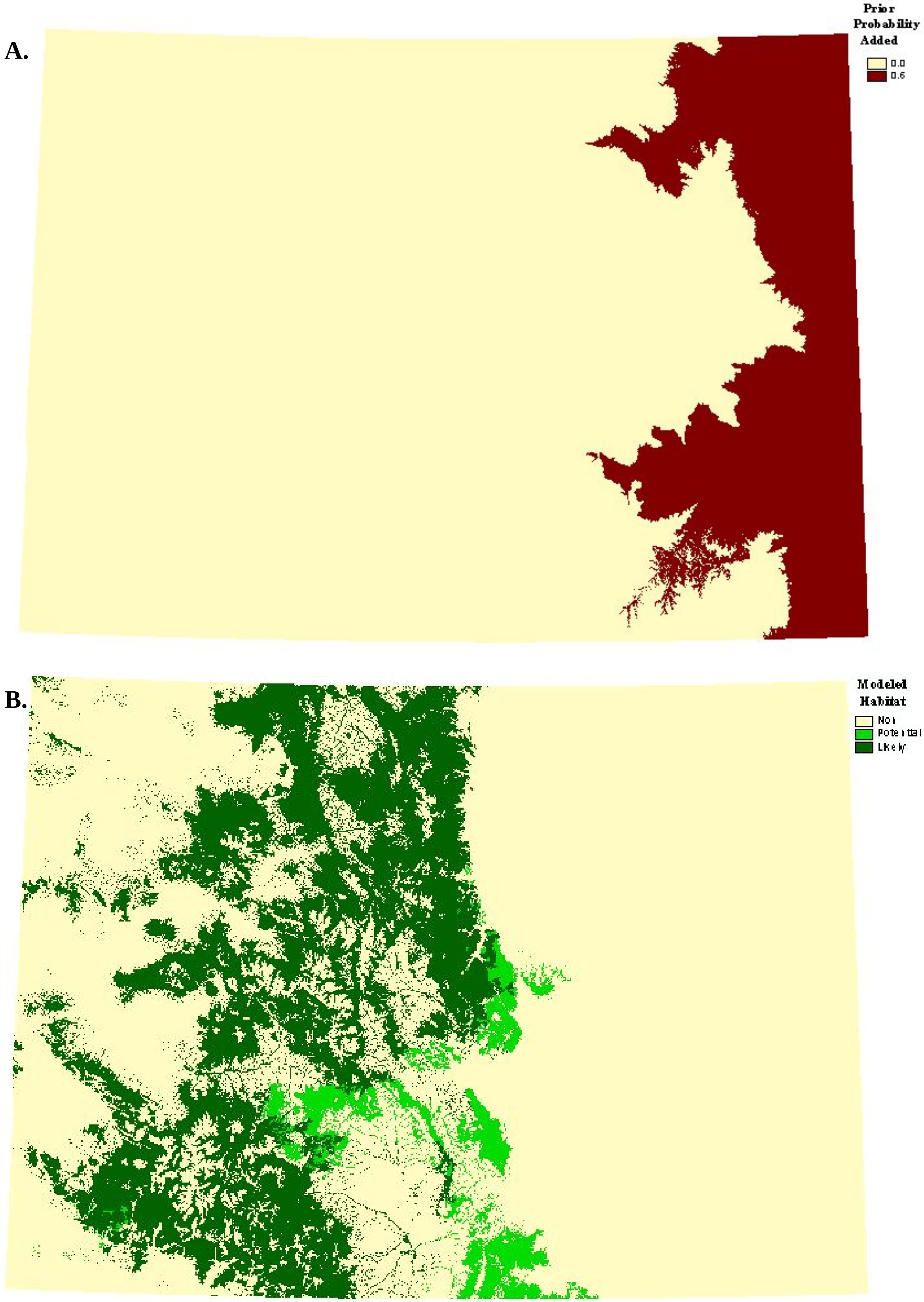


Figure 36. Sensitivity of Model to Prior Probability Surface. Altered prior probability (A) added to boreal toad prior model (B) used to test the model sensitivity to prior probabilities.

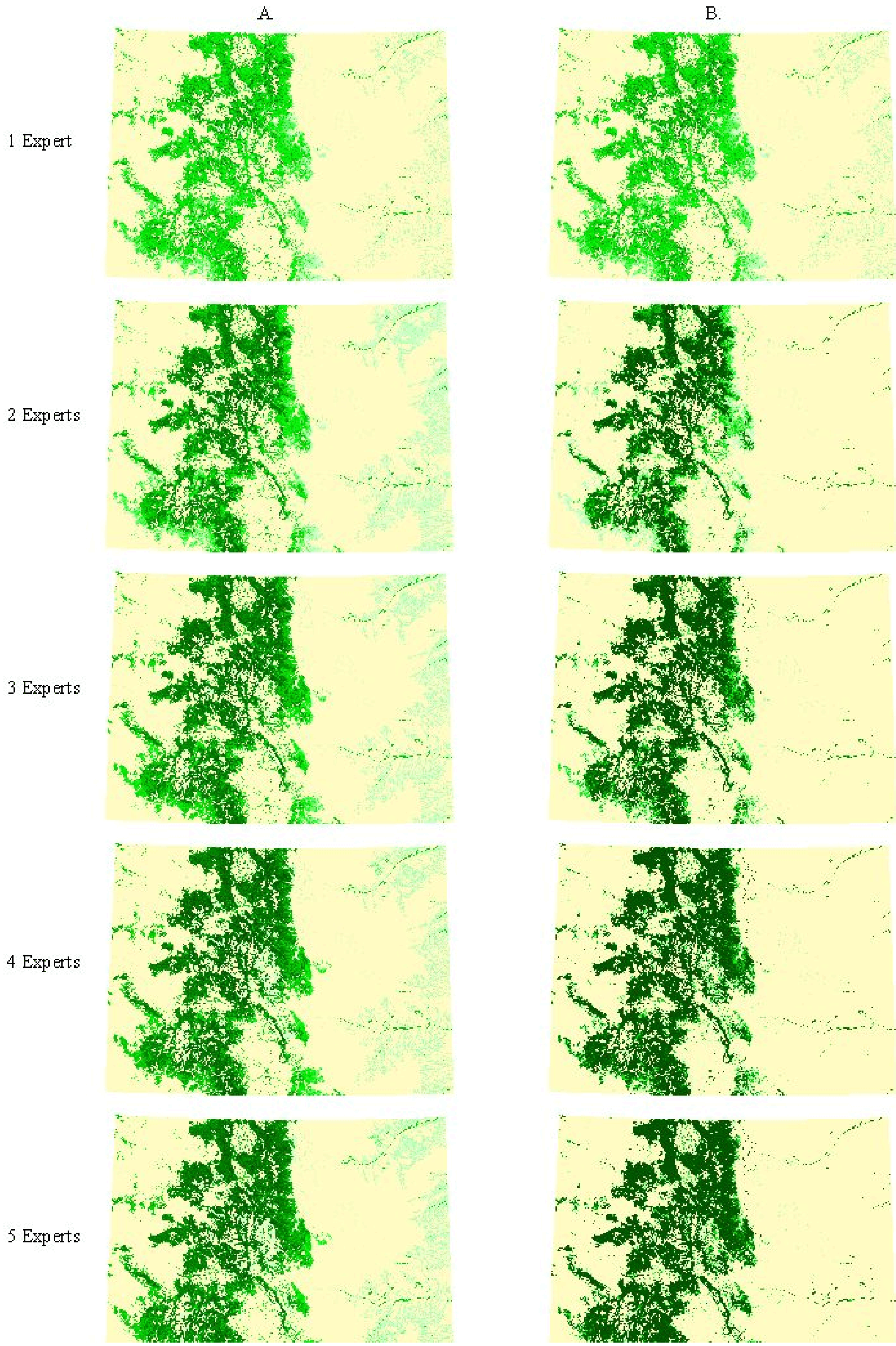


Figure 37. Sensitivity of Model to Altered Prior with Averaged Expert Opinions vs Iterative Bayes' Calculations. Posterior probability surfaces with expert opinions averaged (A) and used as the priors in iterative Bayes' calculations (B) starting with the altered prior probability surface.

had a slight effect on the model. The further the prior probabilities were from 0.5, the non-informative prior, the larger the effect of altering their values.

The last method used to test the sensitivity of the models to the prior probabilities was to alter all the prior probability assignments simultaneously, so the that the prior probability surface had uniform probability values of 0.0, 0.1, 0.3, 0.5, 0.8 and 1.0. The results of this analysis (Figure 38, Column D) showed that indeed the prior probability again had a major effect on the resulting posterior probability surface, overwhelming the information provided by one species expert at the extreme vales of 0.0 and 1.0.

The last sensitivity test of the modeling procedure was done to ascertain the effect of species experts assigning non-informative priors (0.5) to areas they felt that they did not have enough knowledge about to assign more informative probability values to. An area of the geographic range probability surface for the boreal toad that had been assigned a probability of 0.0 by a species expert was changed to 0.5 and the Bayesian calculations were re-run (Figure 39). The result of reassigning the habitat association probabilities were negligible (Figure 40).

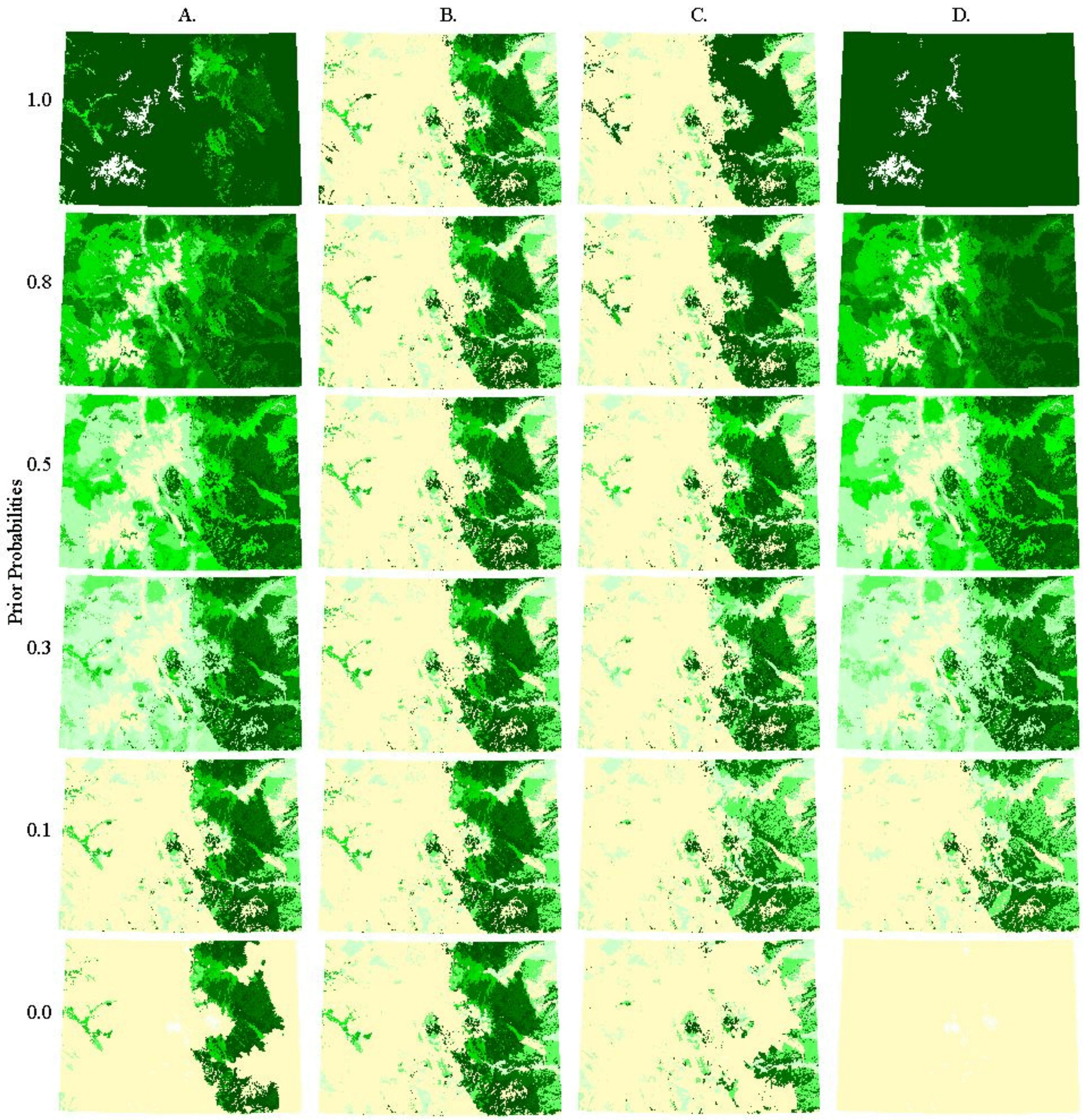
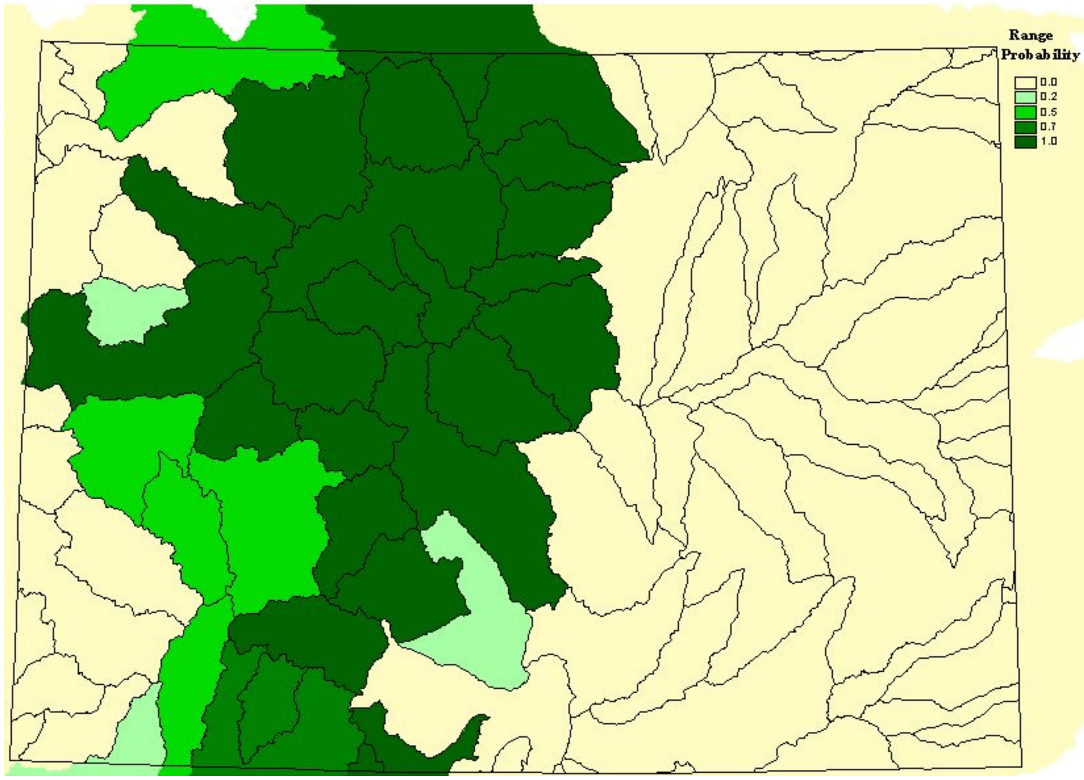


Figure 38. Sensitivity of Model to Altered Prior Probabilities. A comparison of mountain plover posterior probability surfaces in which prior probabilities were altered across a range of values. Non (A), potential (B) and likely (C) habitat categories were changed from their original prior probability assignments of 0.1, 0.5 and 0.6 respectively to the values along the left side of the figure, while the other 2 categories were held constant. In Column D, the prior probabilities were simultaneously changed to the values along the left side.

A.



B.

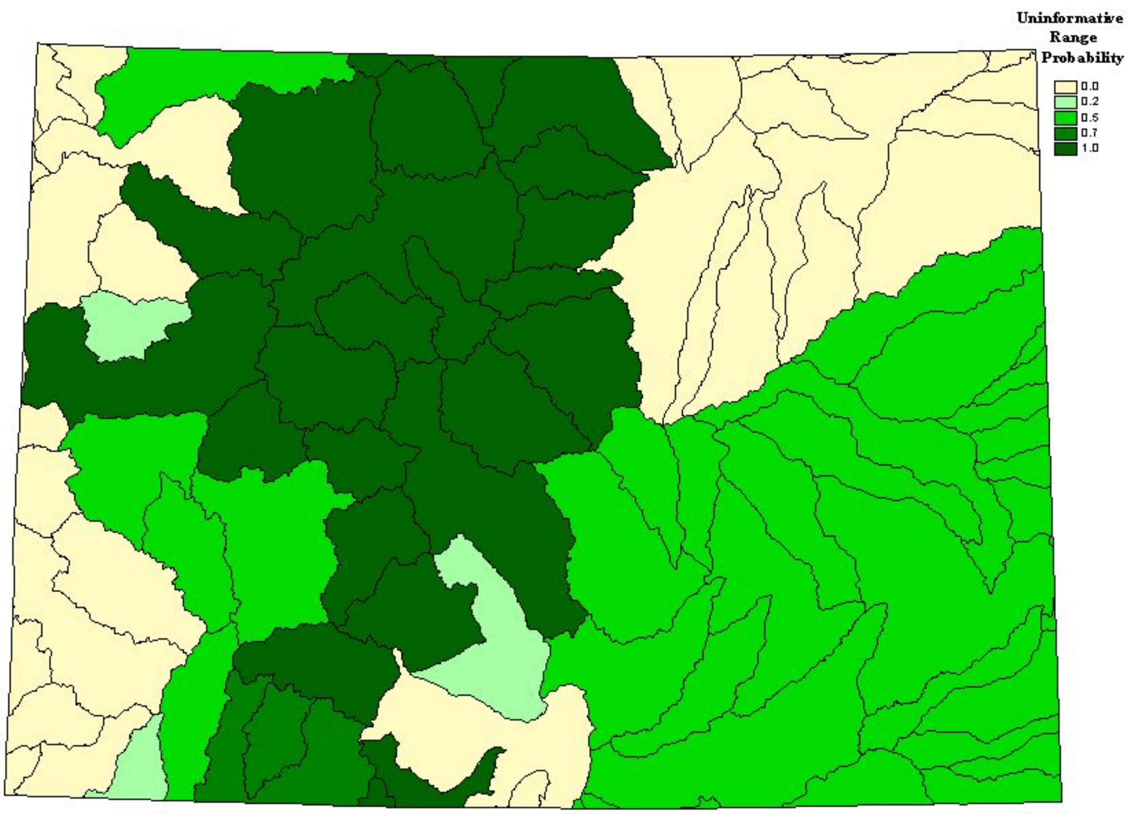


Figure 39. Adding Non-informative Probabilities to Model. The geographic range probability surface for the boreal toad (A) after being altered (B) by changing an area from probabilities of 0.0 to 0.5 (the non-informative probability value).

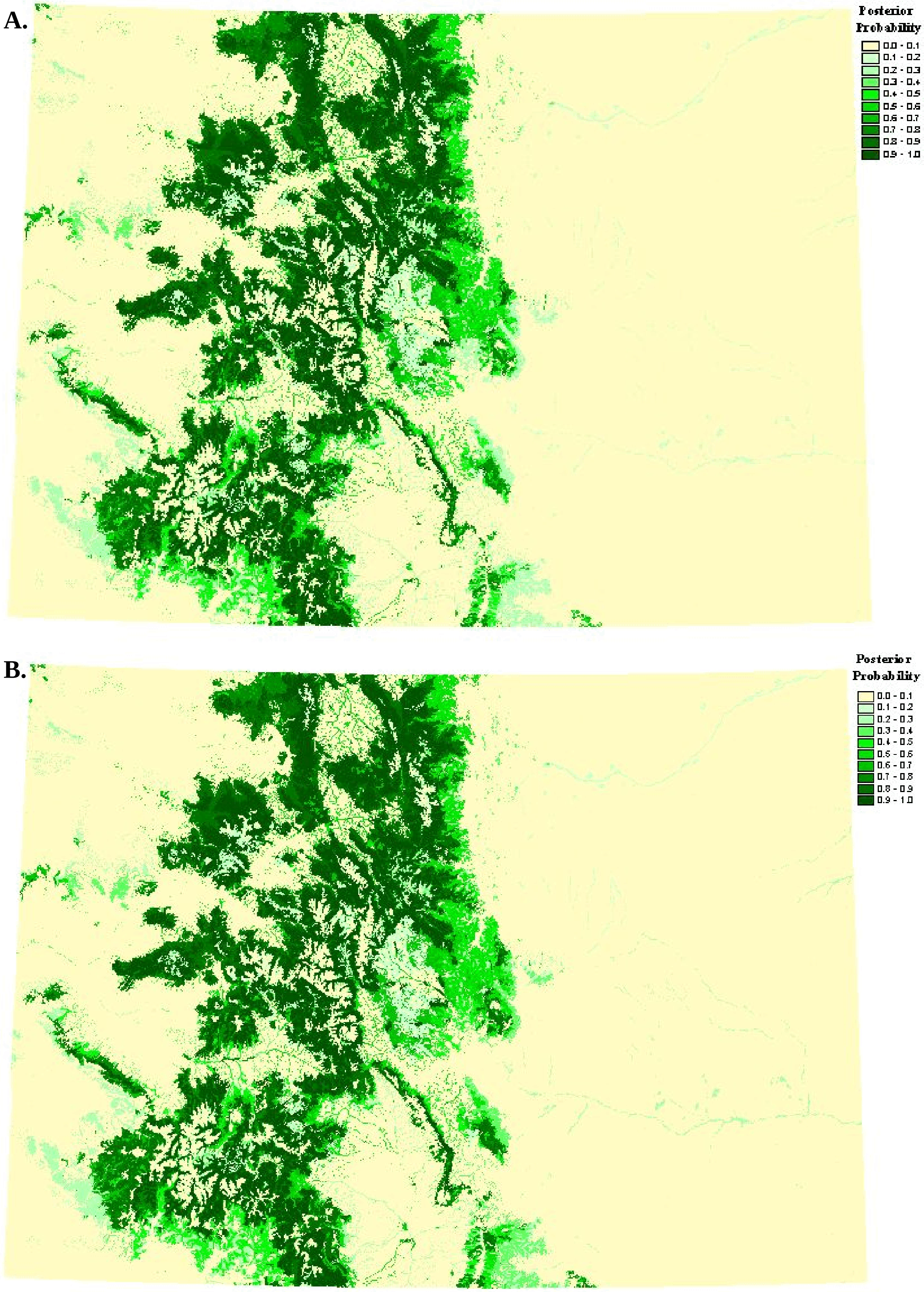


Figure 40. Sensitivity of Model to the Addition of Non-informative Probability. Boreal toad posterior probability surfaces without (A) and with (B) altered range probabilities in lower right corner.

CONCLUSION

Allowing uncertainty to delay decisions to protect biodiversity is to make a tacit decision to allow and thereby promote the status quo; no decision is in fact still a decision.
– John Lemons 1996

The method of developing habitat suitability models proposed in this study, by updating prior habitat models with species expert opinions using Bayesian techniques, was found to be simple to implement and easy for experts to understand. It also produced models incorporating uncertainty that were transparent and easy to interpret. Once the tools for reviewing prior models and collecting expert opinions were completed and the methods for calculating Bayes' Theorem with raster GIS grids was automated, collecting the required data and running the models was quick and easy.

Being knowledge-based models, not reliant upon species occurrences to derive habitat associations, these models avoid the problems associated with attempting to derive habitat associations from species occurrences. The models are derived from the opinions of species experts and they are designed to be periodically reviewed and updated with new knowledge, continually making them better. In areas where species experts agree, the certainty of the predictions will go up and in areas where experts disagree, certainty will go down. Over time, the models will reflect the state of knowledge about the distribution of a species' suitable habitat.

The models developed via this method predict the distribution of suitable habitat, not species occurrence or abundance. These are the "container habitats" that O'Connor (2002) speaks of, somewhat disparagingly. Because the models do not attempt to predict where species will occur at any point in time, they cannot be evaluated by comparisons to species occurrences. They are evaluated by how credibly they represent the current accumulated knowledge about a species habitat and how useful they are to habitat managers and planners.

To determine their credibility, the models are examined in light of Rejeski's (1993) four issues that must be addressed in establishing credibility:

1) Believability – are the models and supporting data properly chosen?

2) Honesty – have uncertainties inherent in the analysis been conveyed?

3) Decision Utility – does the analysis provide a clear basis for action?

4) Clarity – are the maps understandable and sensitive to perceptual differences of the intended audience?

A question that arises with Bayesian inference is whether the subjective nature of the information compromises credibility (Dennis 1996). The habitat models are sensitive to prior probabilities. However, these are knowledge-based models based upon and reflecting the state of knowledge about the distribution of suitable habitat. Prior information is an important part of the Bayesian method, thus it is important to obtain the best information available and represent this information accurately when deriving prior probabilities. The believability of the models, Rejeski's first criterion for credibility, is maintained by the incorporation of the latest combined expertise of species experts, by the fact that they can be updated any time new data is uncovered, and by the explicit presentation of the uncertainty inherent in their predictions.

Rejeski's second criterion is honesty. The models created by this method are honest in their depiction of what is known and what is not known (uncertainty) about suitable habitat distributions. By incorporating and depicting the uncertainty inherent in GIS habitat suitability models, the models satisfy a main critique of these type of models, that their credibility cannot be judged because they do not reveal their inherent uncertainty

(Conroy and Noon 1996; Dean et al. 1997; Flather et al. 1997). The models incorporate the uncertainty in the species habitat associations, the uncertainty in experts' knowledge, the uncertainty in introducing landscape context and, when available, they can incorporate the uncertainty in the underlying GIS datasets. Depicting the uncertainty associated with suitable habitat predictions is imperative for users of the models to understand the strengths and limits of the models. Revealing inherent uncertainty is the primary reason the models were designed around Bayes' Theorem.

At a time when one of the greatest contributors to loss of biodiversity is loss of habitat (Wilson 1988), the models can serve to locate where important habitats are, regardless of whether they are presently occupied. They can be used in conservation planning to save the containers, if you will. Models constructed in this manner were also shown to include potentially important habitat that was missed by models based upon strict (yes/no) a priori decisions. The utility of the models, Rejeski's third criterion, is also enhanced by the fact that users of the models know where model predictions are strong and where they are weak. This information is useful for planning and can be used to guide further research.

Clarity, Rejeski's final criterion for credible models, is provided by their simplicity and easy interpretation. Bayesian probabilities can be straightforwardly interpreted as what is known (certainty) about an unknown parameter or event, suitable habitat in this case. In contrast, a traditional or "frequentist" interpretation of probability is "the limit of the relative frequency with which an event occurs in a series of suitably relevant observations in which the event could occur" (Luce and O'Hagan 2003). This is much more difficult for managers or planners to comprehend. Since the goal of creating habitat suitability models is to provide planners and managers honest and useable information on which to make informed decisions, an easily interpreted, simple model is better, as long as it is credible.

The models derived by this method appear to meet all of Rejeski's criteria for deeming models credible. The method produces a simple, honest, spatial depiction of what is known about the distribution of suitable wildlife habitat that can be used to support more informed decisions in species conservation planning and management. The resulting posterior probability surfaces can also be used to target further studies of species habitat use, guide hypothesis tests about species distribution, or used in adaptive management scenarios. The information gained from these studies can be rolled back into the models to update the state of knowledge about the predicted distribution of suitable habitat (Figure 41).

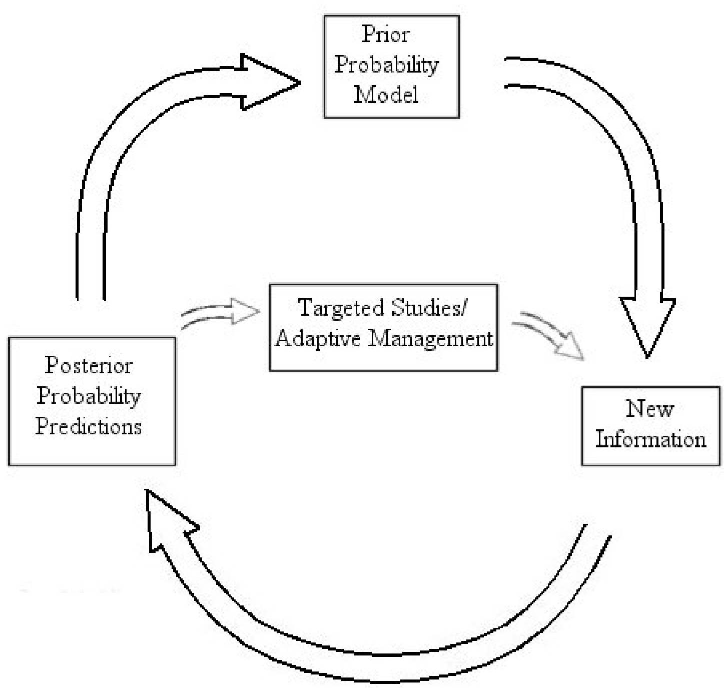


Figure 41. Integrating Bayesian Method with Empirical Studies. This method can be used to guide empirical studies and then incorporate the new data into the models.

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APPENDIX A

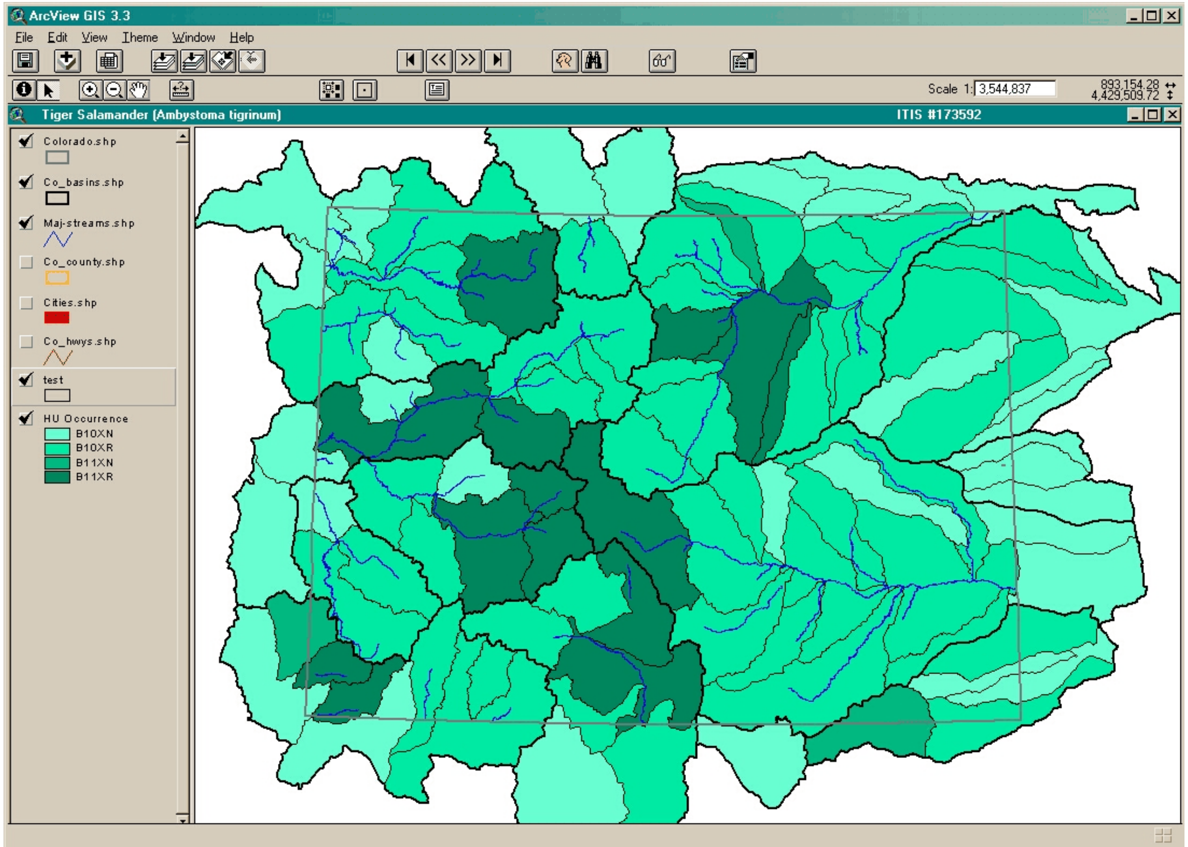
INSTRUCTIONS FOR ESRI ARCVIEW RANGE REVIEW

AND MS EXCEL HABITAT RELATIONSHIP REVIEW TOOLS

Instructions for ArcView - Species Range Review Tool

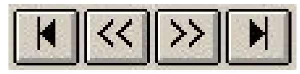
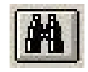
To Begin:

- You must have ESRI ArcView to run this application.
- Create a c:\Review directory on your hard drive.
- Copy all of the application files into this directory.
- Open "Review.apr" in ArcView; it should look like this:

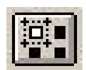
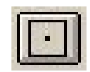


To Review Species Ranges:

- To start, select/create a table to collect all of the edits you will make, by:
  - Clicking the 'Reviewer Data' button: 
  - Select "New Table" and name it after yourself (e.g., yourname.dbf). The table/theme should show up in the Table of Contents area on the left side of the screen.
  - You only have to do this once. To edit data thereafter, make sure that this theme is selected (shown as raised box)

- Select the species that you want to review, by:
  - Species are in taxonomic order (amphibians, reptiles, birds, mammals). You can navigate to the desired species using the VCR buttons: 
  - You can select a species from the species list using the ‘Select Species’ button: 
  - Or, you can search for a species using the ‘Find Species’ button: 

- A range map will be displayed for the selected species. To review the data used to create this map click on the ‘Text’ tool:  and click on a hydro-unit.
- To display a look-up table describing the latilong codes use the ‘LUT’ button: 

- Add range extents by selecting hydro-units and entering a value using the ‘Select Multiple Hydro-Units’ tool:  or the ‘Select Single Hydro-Unit’ tool: 

- Note: to use the Multiple Hydro-Units tool, click on the tool, then click and drag the ‘box’ cursor to create a box. All hydro-units that the box touches will be selected and receive the value you enter. Please try to provide a value for every hydro-unit, replacing all the hatch marks.

- You are asked to review the range maps and add your opinion about the range of the species, by selecting hydro-units and providing a value for how certain you are that the species habitat can be found in the selected hydro-units. The value entered should be between 0 and 1 inclusive, with **0 meaning that you are absolutely certain the species habitat does not occur in the hydro-unit and 1 meaning that you are absolutely certain that the species habitat does occur in the hydro-unit. A value of 0.5would indicate that you are not certain whether the species habitat occurs in the hydro-unit or not.** The value should reflect both your knowledge about the particular species and how certain you are that habitat important for some part of its life history occurs in a particular hydro-unit.

- Ancillary themes such as roads, counties, rivers, etc. can be checked on and off to assist with orientation. Selecting one of these themes and using the ‘Identify’ tool:  will identify the feature (road, county, city, etc.) selected.

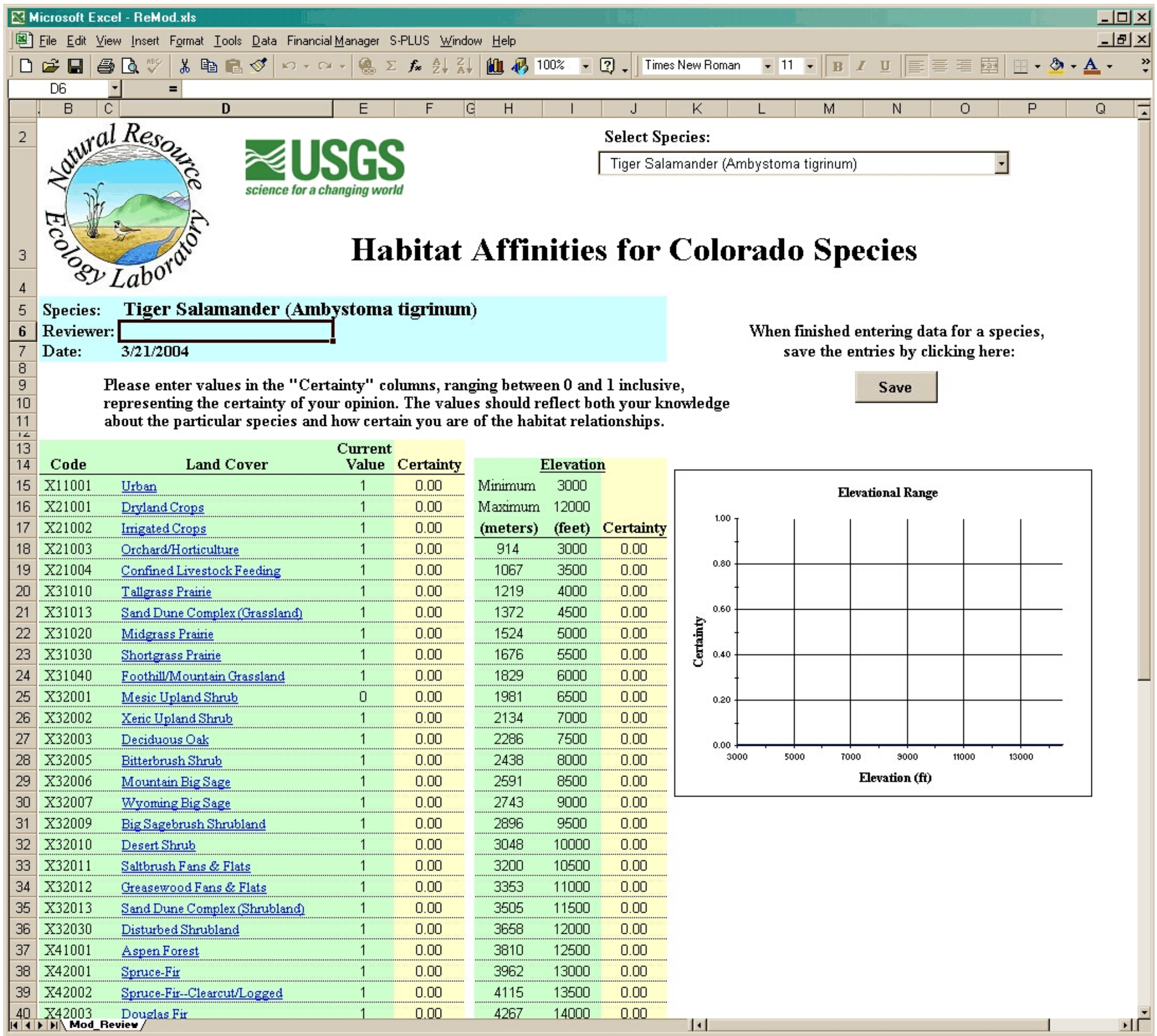
When Finished:

- E-mail the “yourname.dbf” file in the c:\Review directory to: ...

Instructions for MS Excel - Wildlife Habitat Relationship Review Tool

To Begin:

- You must have Microsoft Excel to use this review tool.
- Create a c:\ReMod directory on your hard drive.
- Copy the “ReMod.xls” file and the “lc” folder into this directory.
- Open “ReMod.xls” in MS Excel (you have to enable macros); it should look like this:



Code	Land Cover	Current Value	Certainty	Elevation (meters)	(feet)	Certainty
X11001	Urban	1	0.00	Minimum	3000	
X21001	Dryland Crops	1	0.00	Maximum	12000	
X21002	Irrigated Crops	1	0.00	(meters)	(feet)	Certainty
X21003	Orchard/Horticulture	1	0.00	914	3000	0.00
X21004	Confined Livestock Feeding	1	0.00	1067	3500	0.00
X31010	Tallgrass Prairie	1	0.00	1219	4000	0.00
X31013	Sand Dune Complex (Grassland)	1	0.00	1372	4500	0.00
X31020	Midgrass Prairie	1	0.00	1524	5000	0.00
X31030	Shortgrass Prairie	1	0.00	1676	5500	0.00
X31040	Foothill/Mountain Grassland	1	0.00	1829	6000	0.00
X32001	Mesic Upland Shrub	0	0.00	1981	6500	0.00
X32002	Xeric Upland Shrub	1	0.00	2134	7000	0.00
X32003	Deciduous Oak	1	0.00	2286	7500	0.00
X32005	Bitterbrush Shrub	1	0.00	2438	8000	0.00
X32006	Mountain Big Sage	1	0.00	2591	8500	0.00
X32007	Wyoming Big Sage	1	0.00	2743	9000	0.00
X32009	Big Sagebrush Shrubland	1	0.00	2896	9500	0.00
X32010	Desert Shrub	1	0.00	3048	10000	0.00
X32011	Saltbrush Fans & Flats	1	0.00	3200	10500	0.00
X32012	Greasewood Fans & Flats	1	0.00	3353	11000	0.00
X32013	Sand Dune Complex (Shrubland)	1	0.00	3505	11500	0.00
X32030	Disturbed Shrubland	1	0.00	3658	12000	0.00
X41001	Aspen Forest	1	0.00	3810	12500	0.00
X42001	Spruce-Fir	1	0.00	3962	13000	0.00
X42002	Spruce-Fir--Clearcut/Logged	1	0.00	4115	13500	0.00
X42003	Douglas Fir	1	0.00	4267	14000	0.00

To Review Wildlife Habitat Relationships:

- Enter your name in the “Reviewer” box and select the species to review from the drop-down box in the upper right corner.

- You are asked to add your opinion about the habitat relationships of the species in the yellow “Certainty” columns, by providing a value for how certain you are that the habitat element listed is associated with suitable habitat for the selected species.

- The value entered should be any value between 0 and 1 inclusive, with **0 meaning that you are absolutely certain the habitat element is not associated with suitable habitat for the species, and 1 meaning that you are absolutely certain the habitat element is associated with suitable habitat for the species. A value of 0.5 would indicate that you are not certain whether the habitat element is associated with suitable habitat or not.** The value should reflect both your knowledge about the species and how certain you are that the habitat elements are part of the species' suitable habitat. Please review each habitat element and make sure there are values for all landcover and elevation relationships and, if proximity to water is important, values for those relationships (if proximity to water is not important, leave those values as all 0's).

- The "Current Values" in the green boxes are the values that were used in the original habitat models. They are listed for reference purposes only.

- Clicking on a landcover code will open a PDF description of the landcover type, clicking on a landcover name will open a pop-up map showing the distribution of that landcover type.

- When you have completed entering certainties for all habitat relationships for a species, click the "Save" button and the program will copy your data to a separate worksheet and reset the data entry worksheet. It will be ready to accept data for a new species.

When Finished:

- E-mail the "ReMod.xls" file in the c:\ReMod directory to: ...

APPENDIX B

PROCEDURES FOR CONVERTING EXPERT OPINION DATA INTO PROBABILITY SURFACES

Procedures for Creating Input Themes for Bayesian Computation

Step 1 - Creating Old Species Model (Prior Probability) Theme
- Obtain original COGAP habitat model (grid)
- Add a 4 digit numerical field ("Index") for reclassifying 0 to 100, 1 to 500 and 2 to 600
- Run Grid Reclass (script) on this grid, selecting the "Index" field for new grid cell values
- Rename "Index" grid as "prior"... species model

Step 2 - Creating New Landcover Probability Theme
- Copy landcover columns of Excel model review tool for species to separate worksheet
- Multiply the responses by 1000, save the worksheet as a dbf table and import into ArcView
- Join this table to the CO_lc shapefile and copy to a grid using 1000 x responses as cell values

Step 3 - Creating Elevational Range Probability Theme
- Add a 4 digit numerical field to the CO_elev grid for reclassifying elevations to expert opinions
- Add expert review values (x 1000) to the field based upon cut off elevation values
- Run Grid Reclass (script) on this grid, selecting the reclass species field for new grid cell values

Step 4 - Creating Geographical Range Probability Theme
- Copy the species expert range review to a new shapefile in the ArcView Range Review Tool
- Import this shapefile into the Bayes ArcView session
- Add a 4 digit numerical field and populate it with the review values x 1000
- Copy this shapefile to a grid using the 1000 x responses field as cell values

Step 5 - Creating Proximity to Water Probability Theme
- Add a 4 digit numeric field to the Waterbuff grid for reclassifying water buffers to probabilities
- Add expert review values (x 1000) to the field based upon cutoff proximity to water values
- Run Grid Reclass (script) on the grid, selecting the new field for new grid cell values

APPENDIX C

ESRI ARCVIEW AVENUE SCRIPTS FOR

CREATING GRIDS FROM FIELDS IN EXISTING GRIDS AND

RUNNING BAYESIAN GRID CALCULATIONS

```
'******************************************************************************
'*  Script Name = Grid Reclass
'*
'*  This script creates a new grid from a field in the attribute table of an existing grid with cell
'*  values for the new grid coming from the field in the old grid.
'*
'*  01-30-04 - Lee O'Brien, Natural Resource Ecology Lab
'******************************************************************************

deBug = false

if (deBug) then
  thisProject = av.GetProject
  theView = thisProject.FindDoc ( "Remod_View" )
else
  theView = av.GetActiveDoc
end

' select old grid
thmList = theView.GetThemes
oldGTheme = MsgBox.List (thmList, "Select grid to create new grid from:", "Select Grid")
if (oldGTheme = nil) then return nil end

while (oldGTheme.Is(GTHEME).Not)
  MsgBox.Error ( "This procedure only works on grids. Please select again.", "")
  oldGTheme = MsgBox.List (thmList, "Select grid to create new grid from:", "Select Grid")
  if (oldGTheme = nil) then return nil end
end

oldGrid = oldGTheme.GetGrid

oldGrid.BuildSTA

if (oldGrid.HasError) then
  MsgBox.Info("oldGrid.HasError = TRUE", "ERROR")
  return NIL
end

oldVTab = oldGrid.GetVTab

' select field to create new grid from
theFlds = oldVTab.GetFields
theFld = MsgBox.List (theFlds, "Select field to create new grid values from:", "Select Field")
if (theFld = nil) then return nil end

'create new grid
```

```
newGrid = oldGrid.Lookup ( theFld.AsString )

newGrid.BuildSTA

if (newGrid.HasError) then
  MsgBox.Info("newGrid.HasError = TRUE", "ERROR")
  return NIL
end

newGTheme = GTheme.Make ( newGrid )
newGTheme.SetName ( theFld.AsString )
theView.AddTheme ( newGTheme )
```

```
'**************************************************************************
'*  Script Name = Bayes Calculation
'*
'*  This script combines prior and habitat suitability probability grids for a species using
'*  Bayes Theorem to create a posterior probability grid, depicting uncertainty in the
'*  species habitat suitability model.
'*
'*  09-09-03 - Lee O'Brien, Natural Resource Ecology Lab
'*  03-20-04 - Lee O'Brien - made program generic, so any number of grids can be used
'**************************************************************************

deBug = false

if (deBug) then
  thisProject = av.GetProject
  theView = thisProject.FindDoc ( "Remod_View" )
else
  theView = av.GetActiveDoc
end

' get species
sp = MsgBox.Input ( "Enter the name of the species to run model on:", "Bayes Model",
"species name" )
if (sp = nil) then return nil end

intTxt = MsgBox.Input ( "The probability grids used in this calculation have to be integer grids.
Enter the factor you used to convert probability values to integers:", "Integer Conversion
Used", "1000" )
if (intTxt = nil) then return nil end
int = intTxt.AsNumber

thmList = theView.GetThemes

' select prior probability grid
priorGTheme = MsgBox.List (thmList, "Select the preliminary habitat model (prior
probability) grid:", "Select Grid")
if (priorGTheme = nil) then return nil end

while (priorGTheme.Is(GTHEME).Not)
  MsgBox.Error ( "This procedure only works with grids. Please select again.", "")
  priorGTheme = MsgBox.List (thmList, "Select the preliminary habitat model (prior
probability) grid:", "Select Grid")
  if (priorGTheme = nil) then return nil end
end

priorGrid = priorGTheme.GetGrid
```

```
new = TRUE
namList = List.Make
cnt = 0

while (true)
  ' select habitat suitability grids
  hsGTheme = MsgBox.List (thmList, "Select a habitat suitability grid to use in the calculation
of conditional probabilities:", "Select Grid")
  if (hsGTheme = nil) then return nil end

  while (hsGTheme.Is(GTHEME).Not)
    MsgBox.Error ( "This procedure only works on grids. Please select again.", "")
    hsGTheme = MsgBox.List (thmList, "Select a habitat suitability grid to use in the calculation
of conditional probabilities:", "Select Grid")
    if (hsGTheme = nil) then return nil end
  end

  nam = hsGTheme.GetName

  hsGrid = hsGTheme.GetGrid

  wtTxt = MsgBox.Input ("What weight should be given to the " + nam + " grid?",
"Weighting", "1")
  if (wtTxt = nil) then return nil end
  wt = wtTxt.AsNumber
  cnt = cnt + wt

  ' combine habitat suitability grids into a cumulative suitability grid with weights
  if (new) then
    cumGrid = hsGrid * wt.AsGrid
  else
    cumGrid = cumGrid + (hsGrid * wt.AsGrid)
  end

  ' combine habitat suitability grids into a cumulative unsuitability grid with weights
  if (new) then
    cumunGrid = (int.AsGrid - hsGrid) * wt.AsGrid
  else
    cumunGrid = cumunGrid + ((int.AsGrid - hsGrid) * wt.AsGrid)
  end

  namList = namList.Add( nam + " (x" + wt.AsString + ")" )

  showList = MsgBox.ListAsString( namList, "List of grids to be used in Bayes' calculation:",
"Grid List" )
  if (showList = nil) then return nil end
```

```
  again = MsgBox.YesNoCancel ( "Add another habitat suitability grid?", "Add Grid", TRUE )
  if (again = nil) then return nil end
  if (again.not) then break end
  new = FALSE
end

'calculate average of habitat (un)suitablity grids for conditional probability grids
suitGrid = cumGrid / cnt.AsGrid
unsuitGrid = cumunGrid / cnt.AsGrid
unpriorGrid = int.AsGrid - priorGrid

' use Bayes Theorem to create posterior probability grid
postGrid = ( priorGrid * suitGrid * int.AsGrid ) / ( (priorGrid * suitGrid) + ( unpriorGrid *
unsuitGrid ) )

postGrid.BuildSTA

if (postGrid.HasError) then
  MsgBox.Info("postGrid.HasError = TRUE", "ERROR")
  return NIL
end

postGTheme = GTheme.Make ( postGrid )
postGTheme.SetName ( sp + "_pp" )
postLegend = postGTheme.GetLegend
postLegend.Load ("finalpp.avl".AsFileName, #LEGEND_LOADTYPE_ALL)
postGTheme.UpdateLegend

theView.AddTheme ( postGTheme )
```

APPENDIX D

FUZZY VALUES FROM LANDCOVER ACCURACY ASSESSMENT

Results of the RIGHT fuzzy operator evaluation in the fuzzy accuracy assessment of the Colorado Gap Analysis landcover map, adapted from Reiners et al. (2000). Percent Matches are the proportion of map polygons for which the correspondence with the video reference data is considered "reasonable or acceptable" for animal habitat models. Grid Values are Percent Matches converted into probabilities multiplied by 1000 for entry into integer grid cells. Values of “NA”, insufficient data, were given probabilities of 0.5 (Grid Value 500), non-informative probability values.

Reiners ID	GAP Code	Landcover Type	Percent Match	Grid Value
52	11001	Urban	77.78	778
40	21001	Dryland Crops	82.76	828
41	21002	Irrigated Crops	72.00	720
42	21003	Orchard/Horticulture	NA	500
43	21004	Confined Livestock Feeding	NA	500
32	31010	Tallgrass Prairie	80.95	810
35	31013	Sand Dune Complex (Grassland)	90.00	900
33	31020	Midgrass Prairie	74.19	742
34	31030	Shortgrass Prairie	71.74	717
36	31040	Foothill/Mountain Grassland	75.00	750
18	32001	Mesic Upland Shrub	40.00	400
19	32002	Xeric Upland Shrub	63.64	636
15	32003	Deciduous Oak	75.00	750
20	32005	Bitterbrush Shrub	0.00	0
21	32006	Mountain Big Sagebrush	NA	500
22	32007	Wyoming Big Sagebrush	100.00	1000
23	32009	Basin Big Sagebrush	68.75	688
24	32010	Desert Shrub	66.67	667
25	32011	Saltbrush Fans and Flats	9.10	91
26	32012	Greasewood Fans and Flats	53.33	533
27	32013	Sand Dune Complex (Shrubland)	94.12	941
28	32030	Disturbed Shrubland	NA	500
16	41001	Aspen Forest	88.89	889
1	42001	Spruce-Fir	92.59	926
2	42002	Spruce-Fir--Clearcut/Logged	NA	500
3	42003	Douglas Fir	92.59	926
4	42004	Lodgepole Pine	82.35	824
5	42007	Lodgepole Pine--Clearcut/Logged	100.00	1000
6	42009	Limber Pine	NA	500
7	42010	Ponderosa Pine	84.00	840
8	42011	Blue Spruce	NA	500
9	42012	White Fir	NA	500
10	42015	Juniper Woodland	85.71	857
11	42016	Pinyon-Juniper Woodland	72.41	724
12	42017	Rocky Mountain Bristlecone Pine	20.00	200
13	42018	Mixed Conifer	100.00	1000
14	43000	Mixed Forest--General	50.00	500
50	52001	Open Water	100.00	1000
17	61001	Forested Wetlands	60.00	600

Reiners ID	GAP Code	Landcover Type	Percent Match	Grid Value
31	62001	Shrub Dominated Wetlands	75.00	750
39	62002	Grass/Forb Dominated Wetlands	50.00	500
46	70000	Barren Lands	NA	500
49	71001	Unvegetated Playa	NA	500
47	71002	Bare Soil	NA	500
48	73000	Sandy Areas	NA	500
45	74001	Exposed Rock	50.00	500
51	75001	Strip Mines/Quarries	NA	500
29	81001	Prostrate Shrub Tundra	25.00	250
38	82001	Meadow Tundra	85.71	857
37	82002	Subalpine Meadow	93.75	938
44	83000	Bare Ground Tundra	NA	500
30	85000	Mixed Tundra	69.57	696