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Adequacy of Wildlife Habitat Relation Models for Estimating Spatial Distributions of Terrestrial Vertebrates

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Abstract: *In the U.S. National Biological Service's gap analysis, potential distributions of terrestrial vertebrate species are based on the synthesis of wildlife habitat relation data and then modeled using a vegetation cover map derived from Landsat Thematic Mapper imagery. Using long-term species lists from eight National Parks in Utah, we evaluated the adequacy of the wildlife habitat relations data generated by gap analysis in predicting species distributions at landscape scales. Omission and commission error rates were estimated for major taxonomic groups and for each national park. Depending on the taxonomic group, omission error ranged from 0 to 25%, whereas commission error ranged from 4 to 33%. Error rates were highest in amphibians and reptiles and lowest for birds and mammals. In general, the error rate declined as the size of the park increased. The Utah wildlife habitat relation models performed well when used to predict the presence or absence of terrestrial vertebrates in eight national parks in Utah and should provide valuable information for making conservation decisions. They also provide a measure of support for the use of these models within the gap analysis framework. Although it is likely that accuracy of wildlife habitat relation models will vary from state to state, and even considerably within a state, the modeling process seems robust enough to provide a reasonably high level of accuracy for use in conservation planning at the ecoregion level.*

La adecuación de los modelos de relación del hábitat de la vida silvestre para estimar la distribución espacial de los vertebrados terrestres

Resumen: *En el análisis de intervalos del Servicio Biológico Nacional de los Estados Unidos, la distribución potencial de las especies de vertebrados terrestres están basadas en la síntesis de los datos de relación del hábitat de la vida silvestre y en el modelado a partir de mapas de cobertura de vegetación derivados del "Thematic Mapper" de las imágenes "Landsat." Utilizando la lista de especies de ocho Parques Nacionales en Utah, evaluamos la adecuación de los datos de relación del hábitat de la vida silvestre generados por el análisis de intervalos para predecir la distribución de las especies a escala de paisaje. Los porcentajes de los errores de omisión y de comisión fueron estimados para los mayores grupos taxonómicos y para cada Parque Nacional. Dependiendo del grupo taxonómico, el error de omisión estuvo entre el 0 y el 25% mientras que el de comisión osciló entre el 4 y el 33%. Las tasas de error más altas correspondieron a los anfibios y reptiles, mientras que las más bajas fueron para los pájaros y mamíferos. En general, las tasas de error declinaron en la medida en que el tamaño del parque se incrementó. Los modelos de la relación del hábitat de la vida silvestre para Utah se desempeñaron bien cuando fueron utilizados para predecir la presencia o ausencia de los vertebrados terrestres en ocho parques nacionales de Utah y deberían brindar información valiosa para la toma*

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de decisiones en materia de conservación. Estos modelos también proveen una medida de apoyo para la utilización de los mismos dentro del marco del análisis de intervalos. Si bien la exactitud de estos modelos de la relación del hábitat de la vida silvestre varían de un estado a otro, como así también dentro de un mismo estado, el proceso de modelado parece ser suficientemente robusto como para proveer un nivel razonablemente alto de exactitud para que sean utilizados en la planificación para la conservación a nivel de ecoregiones.

Introduction

Biologists have long used knowledge of animal life-history attributes to model animal ecology. A common approach is to model animal habitat by linking known habitat-use patterns with maps of existing vegetation, thereby identifying the spatial extent of important habitat features for use in conservation and management (Verner et al. 1986). These kinds of models transcend a variety of different scales and purposes, ranging from species-specific Habitat Suitability Index models (Schamberger et al. 1982) to multiple-species wildlife-habitat matrices (Verner & Boss 1980) to spatially explicit descriptions of animal distributions for conservation planning (Scott et al. 1987). Kinds and uses of different modeling approaches are outlined in texts by Verner et al. (1986) and Morrison et al. (1992), and they should be examined for additional information on habitat modeling.

As conservation efforts begin placing greater emphasis on landscape scales, there is need to make better use of site- and species-specific habitat relation models in predicting broad-scale spatial distributions of animal species. Much of this need centers on the often conflicting uses of resources on public and private lands and on desires to ensure the continued maintenance of biological diversity. Calls for maintaining biological diversity are an explicit recognition that biological loss occurs at a variety of different levels, ranging from genes to species to biomes. Efforts to maintain this diversity must be applied to all these levels, not just to endangered species (Noss 1991; Scott et al. 1991). Gap analysis is one approach used by the U.S. National Biological Service and cooperating Agencies for assessing the current status of biological diversity at all levels. It provides a systematic approach for evaluating the protection afforded biological diversity in given areas. It uses geographic information systems (GIS) to identify "gaps" in biological diversity protection that may be filled by the establishment of new preserves or changes in land-use practices (Edwards et al. 1993; Scott et al. 1993; Edwards & Scott 1994).

The National Biological Service gap analysis consists of three primary layers in a GIS: (1) the distribution of actual vegetation cover- and land-use types as delineated from satellite imagery; (2) land ownership and management status; and (3) distributions of terrestrial vertebrates as predicted from the distribution of vegetation and known observations. Within the GIS, overlays of an-

imal distribution and land ownership can be used to estimate the relative extent of protection afforded vertebrate animals. A crucial assumption of gap analysis is that mapped vegetation accurately describes the spatial distribution of terrestrial vertebrates. Historically, approaches to mapping species distributions included dot-distribution maps, grid-based maps, hybrid dot-distribution and range maps, and range maps (Scott et al. 1993). These methods rely only on the location of specimens and typically include no information on the ecological conditions, such as vegetation, that favor presence of the species. Using vegetation as a surrogate to model the presence of animals has limitations (Verner et al. 1986; VanHorne & Wiens 1991; Morrison et al. 1992) but does provide enhancement over the traditional approaches to mapping described above. Because the process does not rely only on known locality records, unsampled areas can be included in predictive models. Coupling known locations with those predicted from vegetation can lead to refined maps of species distribution which can then be used for bioregional conservation planning. Given sufficient samples, the distributions can be mapped as a series of probability or density isoclines (e.g., kriging; see Kemp et al. 1989; Schotzko & O'Keefe 1989).

We examine the assumption of gap analysis that mapped vegetation, when linked with wildlife-habitat relation (WHR) models, accurately describes the spatial distribution of terrestrial vertebrates. To assess the potential shortcomings of using vegetation as a surrogate for animal distributions, we compared separately derived species lists from eight national parks in Utah to the predictions generated from Utah gap analysis. Data from the parks were not used during development of the WHR models for Utah gap analysis. Omission and commission error rates were calculated for four major taxonomic groups, amphibians, birds, mammals, and reptiles. Error rates were further explored to determine whether the pattern of error was associated with different animal life-history attributes. Error was also compared to park size to determine if it varied as a function of park area.

Methods

Data on life-history attributes and distributional information for every terrestrial vertebrate in Utah were ob-

tained from a variety of sources, including published and unpublished literature, museum and federal and state agency records on distributions, and individuals with expert knowledge on a particular species (Foster 1988; Foster & Shrupp 1991). Information was collected on a total of 524 species, including 313 birds, 130 mammals, 66 reptiles, and 15 amphibians. Not surprisingly, the exact number of species by taxonomic group varied among agencies with management responsibilities in Utah. Given that gap analysis is a state-based information system, we selected the species list accepted by the State of Utah Division of Wildlife Resources (UT DWR, 1596 W. North Temple, Salt Lake City, UT 84116). This does not imply that life-history and distributional information was not collected on species not included in the UT DWR list. To the contrary, information was collected on all species, including nonbreeding migrant birds, unverified or occasional species, and those few species extirpated from Utah but still found in the Intermountain West (e.g., gray wolf, *Canis lupus*). For purposes of gap analysis, however, and the analyses presented here, only the list recognized by the UT DWR was used.

The information collected on species-specific habitat relations was as detailed as possible. Given uncertainties about the number and types of cover types to be derived from the vegetation mapping, we elected to associate species with recognized cover types during data base creation. These cover types included forest types recognized by the Society of American Foresters (Eyre 1980), potential natural vegetation classes derived by (Kuchler 1964), and land-use classes defined by the UT DWR. Additional data collected included gross distribution of species by latitude-longitude block (birds, Walters & Sorenson 1983; amphibians and reptiles, Schwin & Minden 1979) or county (mammals, Durrant 1952); ecoregion designation (Bailey 1995) with information on slope and elevation; National Wetlands Inventory class (Cowardin et al. 1979) (where appropriate); structural stage for each cover type used by the species; and season of use. Animal-habitat associations were noted for all habitat types, even if the type was clearly outside of Utah and the surrounding Intermountain West. Once the WHR models were complete, wildlife-habitat associations were cross-walked into the mapped cover types (for details on vegetation cover-type mapping and validation see Ramsey et al. 1992, 1993; Edwards et al. (in press); Homer et al. 1995).

Animal distributions were predicted by intersecting gross distribution, elevation, and cover-type associations from the species-specific WHR models. One problem with use of species-habitat associations is the overprediction of the total area potentially occupied by the animal. For example, numerous amphibians had references indicating association with a broadly defined cover type (e.g., blackbrush, *Coleogyne ramosissima*), even though it is clear that this species was principally associated with water bodies found within blackbrush. Similar

problems exist with bats and other cave-dwelling species whose specific habitat is essentially a point location within a broadly defined cover type.

Data from eight national parks in Utah were not included in the development of the WHR models and were reserved to assess the adequacy of the WHR models in predicting the presence of species (Fig. 1). A list of gap-predicted species for each park was created by intersecting cover-type polygons and animal-species distributions based on the WHR models within each park boundary. This list was compared to a park-generated matrix of species observed in each park. Data included in the park species lists were obtained from a variety of sources. These data were compiled using information contained within the park resources, such as wildlife observation cards and faunal collections, if present. We included park-specific unpublished reports and checklists and some published documents (Rado 1975; Atwood et al. 1980). Prior to our use the park species lists were reviewed by researchers who were familiar with the fauna in each of the national parks.

Omission and commission error rates were used as indicators of the strength of the Utah gap analysis WHR models. Errors of omission were defined as the percentage of species not included on the gap-predicted list but present on the corresponding park-generated list. Conversely, an error of commission measured the percentage of species incorrectly included on the gap-predicted

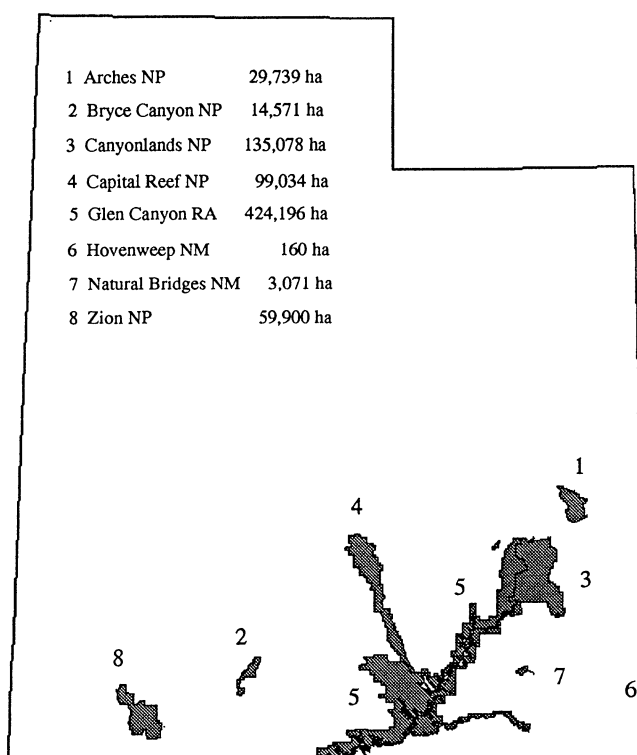


Figure 1. Location and size (ha) of eight park study sites in Utah.

list. Accuracy was defined as the percent of species predicted from the gap analysis models and found in the corresponding park-generated list. Omission and commission error rates were further plotted against park size to determine if error varied as a function of park size. Because information on use of each cover type by each animal species within each park was limited, we were unable to evaluate specific cover-type use by species. Instead, we assessed only the presence or absence of species.

Results

A total of 481 of the 566 state-recognized species (84.9%) was predicted to occur in the eight national parks, representing 15 of 15 amphibians (100%), 315 of 353 birds (89.2%), 110 of 131 mammals (83.9%), and 41 of 67 reptiles (61.2%) in the state. Numbers of species found in the eight parks were 10 amphibians (66.7% of the state list), 282 birds (60.0%), 98 mammals (74.8%), and 46 reptiles (68.6%).

Mean commission and omission error for four major taxonomic groups (amphibians, birds, mammals, rep-

Table 1. Mean and standard deviation (SD) omission and commission error and accuracy of wildlife-habitat relation models predicted by gap analysis by taxonomic group for eight national parks in Utah.

Group	Omission (%)		Commission (%)		Accuracy (%)	
	Mean	SD	Mean	SD	Mean	SD
Amphibians	16.07	8.45	14.51	6.23	69.42	5.41
Birds	1.86	1.33	7.51	4.04	90.63	5.18
Mammals	4.92	1.04	11.50	1.51	83.58	1.07
Reptiles	9.99	1.94	11.57	4.50	78.44	4.59

tiles) in eight national parks in Utah are shown in Table 1. Within parks omission error ranged from 0 to 25% for amphibians, 0.7 to 6.4% for birds, 4.1 to 7.8% for mammals, and 7.2 to 18.8% for reptiles. Omission was lowest for birds and greatest for reptiles. Commission was similarly lowest in birds but was greatest in amphibians rather than reptiles (Table 1). Accuracy ranged from a high of 90.6% for birds to a low of 69.4% for amphibians.

Omission and commission error varied considerably among parks and by taxonomic group (Fig. 2). Overall,

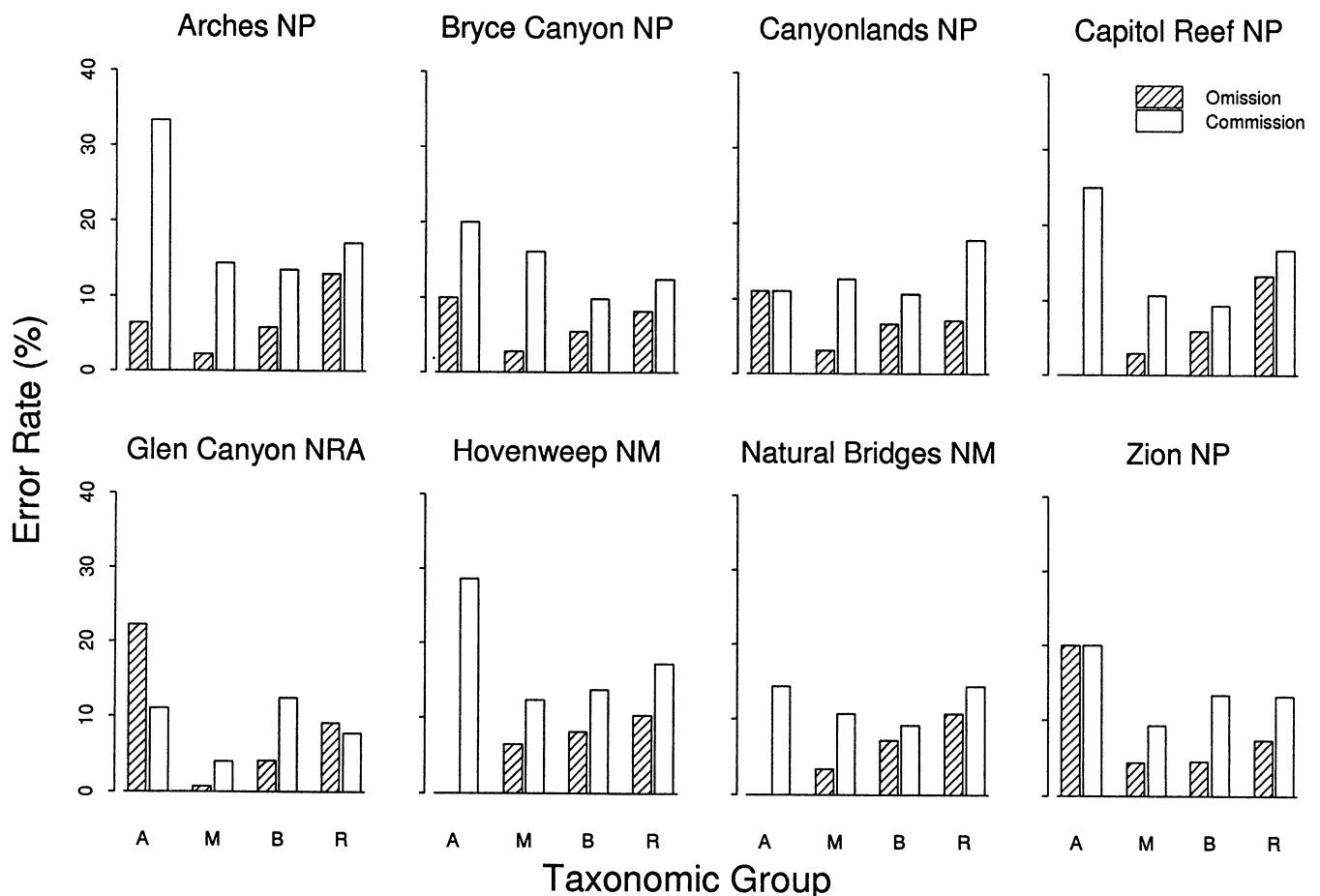


Figure 2. Omission and commission error by national park and taxonomic group (A = amphibians, B = birds, M = mammals, R = reptiles).

commission error was greater than omission error across all parks and taxonomic groups, with the exception of amphibians and reptiles in Glen Canyon National Park (Fig. 2). Within taxonomic group, error rates tended to decrease from amphibians to reptiles to mammals to birds. Overall accuracy by taxonomic group ranged from 60.0 to 85.7% for amphibians, 81.1 to 95.3% for birds, 78.2 to 84.8% for mammals, and 69.9 to 83.2% for reptiles (Table 2).

In general, omission and commission error decreased as park area increased (Fig. 3). Amphibian error was highest, but much of this scatter can be attributed to few amphibians per park (maximum of 11) and the resulting influence of single observations on the error rates. Park-by-park examination of error revealed no pattern based on guilds or other life-history attributes.

Discussion

The National Biological Service's gap analysis process relies on wildlife habitat relation models to link animals to mapped vegetation and then uses vegetation as a surrogate for predicting potential spatial distributions of terrestrial vertebrates (Scott et al. 1993). Once distributions are mapped, the information can be used as a coarse filter for determining locations for new reserves or for other management purposes. Accordingly, an estimate of the uncertainty associated with use of WHR models is critical to use of gap analysis information in determining reserve locations or other management issues (Kareiva 1993).

Our analyses indicate that linkage of WHR models to mapped cover types and the subsequent prediction of vertebrate spatial distributions was fairly reliable in eight national parks in Utah. Accuracy ranged from a high of 91% for birds to a low of 69% for amphibians. Error rates for amphibians and reptiles were greater than for birds and mammals, not an unexpected result given the difficulties associated with inventorying the former two taxonomic groups relative to the latter two groups (see

Heyer et al. 1994), and given a historical emphasis on birds and mammals. Further, data from the parks, although carefully screened by park biologists, were not specifically collected to answer the questions we posed. The lack of design directly linked to our question undoubtedly resulted in undersampling for some rare and localized species, thereby contributing to our overall error rate.

In general, commission error was greater than omission error. This indicates that our models tended to overpredict rather than underpredict the presence of animal species. Given that gap analysis is a tool for predicting geographic distributions of terrestrial vertebrates for use in conservation planning, we argue that commission is preferred over omission. As a measure of uncertainty, commission could arise from many factors, including difficulties in detection among species (Mayfield 1981), bias associated with observers and sampling technique (Bart & Schoultz 1984), problems with rare species, and incomplete species lists from each of the parks we analyzed. Although many of these problems can be overcome by establishment of rigorous inventory designs, it is virtually impossible to apply retroactively a rigorous design to data collected from numerous sources over extensive time periods. From the perspective of conservation planning, commission error can be considered risk-averse. It is better to overpredict rather than underpredict. Omission, in contrast, represents species whose WHR models are inadequate in their predictive ability, and high omission leads to the potential exclusion of species from conservation plans.

Several factors complicate the use of vegetation to predict the presence and absence of species (Scott et al. 1993). Birds, for example, often respond more to vegetation structure than to floristic composition (Cody 1985). Because gap analysis vegetation mapping in Utah relies principally on floristic composition rather than structure, bird distribution maps may contain error. Gap analysis assumes that within floristically defined vegetation classes the structural characteristics necessary to the bird do occur.

Table 2. Number of commission errors (N_c), omission errors (N_o), matches (N_a), and accuracy^a for four taxonomic groups in eight national parks in Utah.^b

Park	Amphibians				Birds				Mammals				Reptiles			
	N_c	N_o	N_a	accuracy	N_c	N_o	N_a	accuracy	N_c	N_o	N_a	accuracy	N_c	N_o	N_a	accuracy
Arches	2	0	4	66.7	25	4	145	83.3	7	3	42	80.8	4	3	16	69.6
Bryce Canyon	1	1	6	75.0	36	6	181	81.3	9	5	77	84.6	3	2	19	79.2
Canyonlands	1	1	7	77.8	28	7	185	84.1	7	5	63	84.0	5	2	21	75.0
Capitol Reef	2	0	6	75.0	25	7	202	86.3	8	5	73	84.9	5	4	21	70.0
Glen Canyon	1	2	6	66.7	11	2	259	95.3	12	4	81	83.5	3	4	32	82.1
Hovenweep	2	0	5	71.4	19	10	126	81.4	7	4	40	78.5	5	3	21	72.5
Natural Bridge	1	0	6	85.7	19	6	152	85.8	6	5	54	83.1	4	3	21	75.0
Zion	2	2	6	60.0	27	13	249	86.2	12	4	74	82.3	5	3	30	78.9

^a Percent accuracy = $[(N_a / (N_c + N_o + N_a))] \times 100$.

^b Results are based on a comparison of gap analysis-predicted and park-observed species lists.

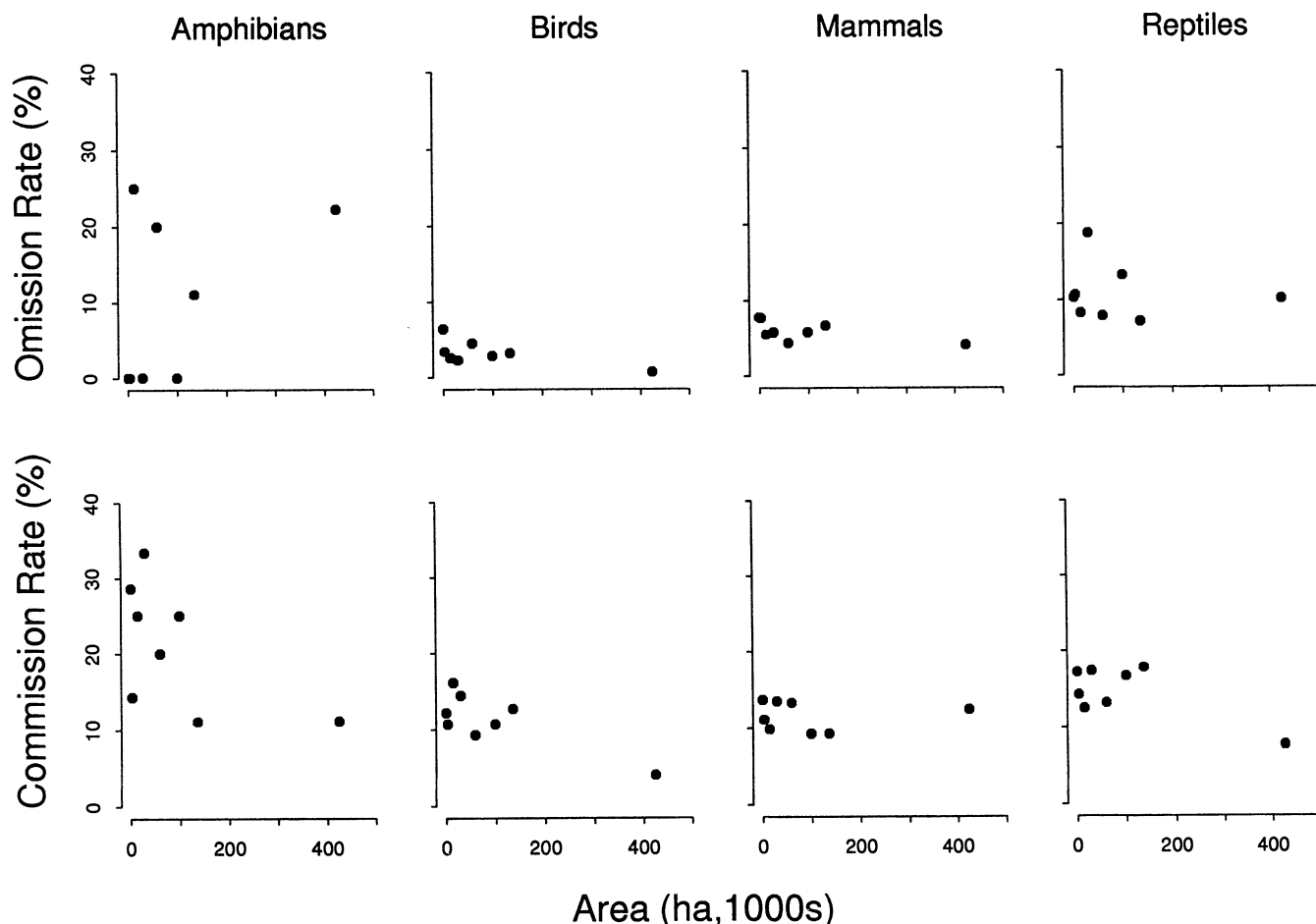


Figure 3. Omission and commission error by taxonomic group and park size (ha).

A second complicating issue is differences in habitat breadth. Some species, like coyotes (*Canis latrans*), are generalists in their habitat. Others are restricted to a single habitat type. If an animal is associated with a single type, and that type can be mapped, gap analysis provides an excellent predictor of range. If the type cannot be mapped because it is below the resolution of the cover map, it is difficult to discriminate from remote sensing techniques, or it is contained in another class, predicted range can be far from actual. Moreover, our ability to map habitat classes often exceeds the natural-history information available for a species. For example, Holland (1986) recognizes 375 plant communities in California. Many of the vegetation units differ only in the ratio of dominant to associated plant species. Although of interest to plant community ecologists, these differences may or may not be of importance to animals.

Although the number of plant communities can be high, natural-history data linking animals to specific communities is sparse for most species. This requires that mapped habitats be grouped into categories that correspond to the known information about a species. For example, the best information on a bird species may

be that it is associated with coniferous forests. Given that at least seven mapped classes in Utah contain conifers, the potential distribution for that species is exceedingly general.

With the exception of amphibians, error rates presented here tended to decline as park area increased. There are several possible reasons for this observation. First, larger parks generally have better inventories of their flora and fauna than smaller parks (Stohlgren & Quinn 1992). Hence, the species lists we used to test our gap-predicted models might be more complete in the larger parks we evaluated, leading to lower error rates. Specifically, more-complete species lists in larger parks would reduce commission error, a generalization supported by our data (Fig. 3). In addition, as area increases the likelihood of "capturing" more rare habitat types increases and the effects of habitat mapping error are likely to diminish. From the perspective of gap analysis, which is targeted at ecoregional levels, this tendency for error to decline as area increases suggests that the species modeling approach used in gap analysis is sufficient when applied to large areas. Extrapolation to local scales is problematic, however, and should be viewed with caution.

Although our analyses indicate that the WHR models were sufficient for predicting species presence in eight national parks in Utah, several problems still exist in evaluating the strength of gap analysis WHR models for Utah. First, no data exist to allow statistical evaluation of specific habitat associations for individual animal species. Our results are restricted to presence or absence within geographic regions only and draw no conclusions about habitat use. Second, our data sets were restricted to the Colorado Plateau region of Utah. No systematically collected and reviewed data exist to permit testing of predicted animal distributions in the Wasatch-Uinta or Basin and Range ecoregions. Thus, the predicted distributions of species not found in the other two ecoregions were not evaluated. Last, the combined effect of spatial error in the vegetation map, error in the WHR models, and error from potentially incomplete species lists in the parks is unknown. How error propagates when numerous information layers in a GIS are involved remains a fruitful area of research (Goodchild & Gopal 1989; Veregin 1989).

A statistically reliable evaluation of specific habitat associations is currently beyond the scope of Utah gap analysis and would require a long-term commitment of resources applied in a statistically rigorous design. Ideally, such efforts should be coordinated with existing federal, state, and private agencies to increase the scope of coverage for an area and to reduce costs and error associated with incomplete inventories like those described by Stohlgren and Quinn (1992). Yet, even with the potential sources of error noted here, use of vegetation as a surrogate for modeling animal species distributions remains a powerful tool for the conservation and management of biological diversity. The Utah WHR models performed well when used to predict the presence or absence of terrestrial vertebrates in eight national parks in Utah and should provide valuable information for making conservation decisions in Utah. They also provide a measure of support for the use of WHR models within the gap analysis framework. Although it is likely that the accuracy of WHR models will vary from state to state and even considerably within a state, the WHR modeling process seems robust enough to provide a reasonably high level of accuracy for use in conservation planning at the ecoregion level.

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