

Influences of roads and development on bird communities in protected Chihuahuan Desert landscapes

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Abstract

Our objective was to improve knowledge about effects of broad-scale road and development variables on bird communities in protected desert landscapes. Bird species richness and the relative abundance or probability of occurrence of many species were significantly associated with total length of roads within each of two spatial extents (1- and 2-km radii), distance to the nearest road, distance to the nearest development, or the two-way interactions of these variables. Regression models reflected non-linear relations, interaction effects, spatial-extent effects, and interannual variation. Road and development effects warrant special attention in protected areas because such places may be important sources of indigenous bird communities in a region.

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1. Introduction

Roads and human development cause significant conservation problems in many nations (Wilkie et al., 2000). Major effects of roads on birds include mortality from roadkills (Mumme et al., 2000), loss of habitat through road construction and fragmentation (Reed et al., 1996), displacement caused by traffic noise (Reijnen et al., 1995, 1996; Forman and Deblinger, 2000), and lower reproductive success associated with increased human access (Trombulak and Frissell, 2000). Development can generate some of the same basic impacts (van der Zande et al., 1980; Odell and Knight, 2001; August et al., 2002 and references therein).

Roads typically traverse many local ecosystems and cover types in the land mosaic (Forman et al., 1997), even in protected areas (Schonewald-Cox and Buechner, 1992); through its association with roads, development also occurs in various places throughout the landscape. Because roads and development are important structural elements of most landscapes, a full understanding

of their ecological influences requires analyses of their effects at broad spatial scales (i.e. within large areas) (see Forman and Hersperger, 1996; Forman et al., 1997). In addition, landscape-wide or larger areas are usually necessary to sustain native bird communities. Therefore, solutions to problems that roads and development cause for bird community conservation will require information about the effects of broad-scale road and development variables.

If complex relations underlie these effects, then knowledge of only simple linear, local-scale, and single-survey associations will not be adequate for understanding and managing the influences. Those responsible for conserving indigenous bird communities need to know whether broad-scale road and development variables influence bird communities positively or negatively, linearly or non-linearly, and additively or interactively. And they need to understand how these relations vary, if at all, across spatial extents and among years.

We studied the combined influences of total road length and the proximity of roads and development on desert bird communities. To our knowledge, the simultaneous and explicit effects of these broad-scale variables on desert bird communities in protected areas

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have not been assessed previously. In some regions, a park, refuge, or other protected area may be an important source of indigenous species. If conservationists expect bird communities in a given area to be maintained or restored through dispersal of native species from protected areas, it is crucial to understand the influences of broad-scale road and development variables in protected areas. This study serves as one example of how to determine such influences.

Whenever feasible, planning and management activities for a protected area should not be based on data from locations that are more disturbed or less disturbed than that protected area, otherwise the amount and spatial configuration of roads and development permitted in the protected area may be over- or under-restricted. Our study characterizes the effects of roads and development for a large protected area in which road width, road density, traffic volume, and development density are considerably lower than those for urban and suburban landscapes.

To advance understanding about the effects of broad-scale road and development variables on bird communities in protected desert landscapes, we addressed the following questions. Do associations between bird metrics (species richness, relative abundance, probability of occurrence) and road or development variables exhibit complexity in the form of non-linear relations, interaction effects, spatial-extent effects, or interannual variation? Is bird community structure associated with broad-scale road and development variables in protected Chihuahuan Desert landscapes? In a companion paper (Gutzwiller and Barrow, 2003), we explain the prospects and constraints of applying the types of models derived in the present analysis.

2. Study area

We conducted this project within Big Bend National Park (BBNP), a 3205 km² Man and the Biosphere Reserve on the Texas-Mexico border (29°19' N, 103°12' W). BBNP lies within the subtropical Chihuahuan Desert and is occupied primarily by igneous grassland (30.6%), limestone grassland (25.4%), and desert shrubland (35.3%). Other land-cover types present are riparian vegetation (4.4%), montane woodland (2.6%), bare ground (1.4%), developed areas (0.2%), and water (0.1%). Characteristic plant species (Whitefield, 1990; Plumb, 1992) for the three main land-cover types were as follows. Igneous grassland: *Bouteloua trifida*, *Muhlenbergia porteri*, *Aristida* spp., *Erioneuron* spp., *Leptoloma cognatum*, *Cathastecum erectum*, and *Hilaria mutica*. Limestone grassland: *Bouteloua gracilis*, *B. hirsuta*, *B. trifida*, *Hilaria mutica*, *Euphorbia antisiphilitica*, *Larrea* spp., *Dasyliion leiophyllum*, and *Hechtia scariosa*. Desert shrubland: *Larrea tridentata*, *Agave lechu-*

guilla, *Opuntia leptocaulis*, *Parthenium incanum*, *Florensia cernua*, *Yucca carnerosana*, *Berberis trifoliata*, *Ephedra aspera*, and *Echinocereus* spp. Previous publications (Wauer, 1971; Plumb, 1992; Gutzwiller and Barrow, 2001) provide details about topography, elevations, soils, rainfall, temperatures, and bird communities.

Park-wide, road density was 0.17 km/km². During the study period (late February–late May), the mean number of vehicles (± 1 S.E.) entering BBNP per day was 459 ± 73 (1995), 407 ± 58 (1996), and 459 ± 70 (1997). The typical combined width of the road surface and adjacent managed verges was ~ 10 m or less, and speed limits of 72 km/h (45 mph) outside of development, and 48 km/h (30 mph) within developed areas, were strictly enforced. No appreciable changes to road length or location have occurred since 1972. Within BBNP, development density was 0.002 km²/km², the size of developed areas was 0.02–2.06 km² (mean = 0.73 km²), developed areas were spaced 0.5–64.6 km (mean = 35.0 km) apart, and the amount and location of development have not changed since the late 1980s.

3. Methods

3.1. Sampling-site establishment

Passable roads extended throughout most of BBNP. Roadsides served as starting points for paths that we used to access our sampling sites. Oriented perpendicular to the road, each path began at the road and ended at the marked centre of a sampling site. To determine the roadside locations of path starting points, we used systematic sampling with a random start (Cochran, 1977). The starting point for the path to the first site was established at a randomly selected distance from the north border of BBNP along the main road. Following the routes of all passable roads, we systematically positioned subsequent path starting points such that the distance between the centres of neighbouring sampling sites was at least 4 km.

Decisions about exact placement of sampling sites were based on the spatial arrangement needed to maximize the number of non-overlapping 4-km-diameter sampling circles (centred on sampling sites) that could be established within BBNP. Using our knowledge of traffic noise and human activity in BBNP, we also based decisions about site placement on distances from roads or development that would prevent traffic noise from interfering with detection of aural cues during bird sampling. All sites were >0.3 km from roads and development; this distance was more than adequate because of the low traffic volume, road density, and development density in BBNP. Site placement also was determined in part by the need to minimize travel time between neighbouring

sampling sites so that bird sampling intensity and the number of sampling sites could be maximized; no site was >0.7 km from a road. The same sampling sites were used during 1995–1997.

3.2. Bird sampling

At the centre of each of 70 sampling sites, 20-min unlimited-distance counts (Ralph et al., 1995) were conducted once each week from late February to late May 1995–1997. This sampling period coincided with the breeding season in our study area (Wauer, 1996). Most sites were sampled 12 times each spring, but because of weather and logistical problems some were sampled five times (six sites, 1995), 10 times (one site, 1996), or 11 times (one site, 1995; one site, 1997). We controlled for variation in the number of counts per site before drawing inferences about road and development effects (see Section 3.5). Data were collected only when wind speed was <20 km/h (Robbins, 1981), air temperature was >0 °C, and no more than a light drizzle was falling. All first counts for a given day began at 0.5 h after official sunrise to avoid potential problems of identifying birds during the dawn chorus, and all final counts were completed before 5.5 h after official sunrise to avoid potential declines in bird activity associated with high air temperature.

In BBNP, vultures, ravens, and raptors, which were typically detected while they were soaring or otherwise on the wing, were detected more frequently during mid to late morning or near mid-day, after the development of thermals or other updrafts (e.g. those caused by wind striking abrupt topography). Most of the species we studied feed on arthropods to some extent during the breeding season, either as gleaners (most species), saliers (especially flycatchers), or species that feed in flight (e.g. nighthawks) (DeGraaf et al., 1991). When early morning temperatures were near freezing, species that feed on arthropods were probably more detectable later in the morning, after their prey became airborne or more active on foliage. Sampling throughout the morning and until around mid-day was thus a more reliable approach for detecting the full complement of diurnal species in our system than was sampling only during early morning. This ability to detect various species was essential because of the community-level focus of the present analysis. To avoid the possibility of biases associated with time-of-day effects, the order in which sites within a local area were sampled was reversed each new week.

Technicians began recording bird data when they reached a marked point that was 50 m from the site centre. This technique enabled them to record birds that were present within the immediate area, but that, in response to the technicians' presence, stopped vocalizing or flushed without returning (Hutto et al., 1986). Technicians

recorded additional bird detections as they walked at a normal pace from the marked 50-m point toward the site centre, where they completed the 20-min count. Technicians considered the timing and location of aural and visual cues, as well as possible unobserved movements, and recorded only those individuals they knew were distinct.

Technicians wore drab clothing to preclude detection biases induced by bright colours (Gutzwiller and Marcum, 1997). Observer effects were controlled in several ways: we employed experienced technicians with excellent hearing and vision (Verner and Milne, 1989); each year technicians spent 2 weeks in BBNP fine tuning their identification skills before data collection began; each technician sampled sites in the major vegetation types in BBNP; and a variable reflecting technician identity (OBSX, where X was the identifying number) was used when necessary in statistical analyses to control for bird-data variation associated with observers.

3.3. Landscape variables

Roads were defined as paved and unpaved surfaces that were regularly used for motor-vehicle travel. In BBNP, several conditions made it impossible to distinguish clearly between the potential for broad-scale disturbance from paved roads and that from unpaved roads. First, traffic volume and speed (hence traffic noise) on some unpaved roads were comparable to those on parts of paved roads; consequently, possible road avoidance due to traffic noise was likely comparable for sections of the two road types. Second, the widths of some paved and unpaved roads were similar, so their respective contributions to habitat loss and fragmentation were probably similar. Third, because paved and unpaved roads provided approximately equal access to trails, potential disturbance from hikers was about the same in landscapes surrounding paved and unpaved roads.

In addition, surface-material differences between paved and unpaved roads generally do not contribute significantly to differences in barrier effects of roads (Forman and Alexander, 1998). For BBNP, the probable overlap of broad-scale effects of paved and unpaved roads on bird communities precluded clear characterization of separate forms of disturbance associated with road type. In our measurements, we did not distinguish between paved and unpaved roads; consequently, our road metrics are general indices of landscape disturbance. We defined development as areas with buildings, parking lots, connecting driveways, landfills, or cleared areas for planned construction.

We created digital maps of roads from 1995, 1:24,000-scale TIGER digital line graph files. A digital map (30×30-m resolution) of development was created from direct knowledge of BBNP development locations (B. Alex,

personal communication). Latitude and longitude coordinates for each sampling site were obtained with 0–1 m accuracy using a global positioning system (GPS) receiver, and these coordinates were used to position sites in digital data layers. We studied road and development variables with the potential to influence bird species richness, relative abundance, and occurrence (Forman and Deblinger, 2000; Odell and Knight, 2001), and the spatial extents we considered are within the range of scales for which significant bird–landscape relations have been found (Van Dorp and Opdam, 1987; Knick and Rotenberry, 1995; McGarigal and McComb 1995; Robinson et al., 1995).

For each sampling site, we used ArcView geographic information system software (Environmental Systems Research Institute, 1998) to measure: total length of roads within each of two spatial extents (1- and 2-km radius circles centred on each site), distance to the nearest road, and distance to the nearest development. All lengths and distances were measured to the nearest 0.01 km. Using techniques described by Neter et al. (1989), we computed the products of pairs of these four variables to obtain data for six two-way interaction effects (Table 1). Interaction effects of these variables have not been quantified previously, and the interdependent nature of ecological systems suggests that interaction effects of roads and development, not simply their main effects alone, may be significantly influential.

Roads and development are not usually distributed randomly across landscapes; in our experience they

often are situated in valleys or along ridgelines, in relatively flat areas, and on well-drained soils. Such environmental conditions can affect the floristic composition and structure of vegetation, which in turn can influence bird community structure. When bird data, road and development variables, and topographic and vegetation conditions are intercorrelated, control for topographic and vegetation effects on bird data is necessary before the influences of roads and development on bird communities can be discerned.

To accomplish this control through our analyses, we measured four environmental variables that covaried with our road variables ($r_s = 0.252$ – 0.429 , $P = 0.0002$ – 0.035 , $n = 70$) and that had the potential to influence bird community structure in our study area (Gutzwiller and Barrow, 2001): elevation of the site, and the percentages of the landscape within 2 km that were covered by igneous grassland, limestone grassland, and desert shrubland (Table 1). We measured elevation to the nearest 5 m with a GPS receiver, and we measured the land-cover variables to the nearest 0.1% with ArcView software. Digital data layers for land cover were based on satellite data with 30×30-m resolution (Whitefield, 1990; Plumb, 1992). Digital geologic data derived from maps in Barnes (1979) were used to distinguish between igneous and limestone grasslands.

3.4. Exploratory analyses

Prior to the present analysis, effects of roads and development on bird metrics had not been examined in our study area. This lack of knowledge about the nature of effects or possible causal relations precluded confirmatory hypothesis testing that was relevant for our system, and it required us to conduct exploratory analyses as a first step to identify potentially important variables. Accordingly, we tested for relations between bird metrics and road and development variables, but we did not test hypotheses about possible biological causes. In the form of empirical models (and the absence of models), our analyses provide initial working hypotheses about bird–road and bird–development relations in our study area. These models can be used to determine the focus of future research into the relations' underlying biological mechanisms (see Gutzwiller and Barrow, 2003).

3.5. Dependent variables

We studied three types of dependent variables. Species richness was calculated as the average number of different bird species, including rare ones, detected per count at a given site within a given year. Relative abundance was computed as the average number of individuals for a given species detected per count at a given site within a given year. The probability of occurrence of a species

Table 1
Road, development, and environmental variables measured at sampling sites in Big Bend National Park, Texas, USA

Abbreviation	Description
R1	Total length of roads within 1 km
R2	Total length of roads within 2 km
NR	Distance from the site to the nearest road
ND	Distance from the site to the nearest development
R1×R2	Interaction between road length within 1 km and road length within 2 km
R1×NR	Interaction between road length within 1 km and distance to the nearest road
R1×ND	Interaction between road length within 1 km and distance to the nearest development
R2×NR	Interaction between road length within 2 km and distance to the nearest road
R2×ND	Interaction between road length within 2 km and distance to the nearest development
NR×ND	Interaction between distance to the nearest road and distance to the nearest development
EL	Elevation of the site
IG	Percentage of the area within 2 km that was covered by igneous grassland
LG	Percentage of the area within 2 km that was covered by limestone grassland
DS	Percentage of the area within 2 km that was covered by desert shrubland

was based on presence-absence data, which reflected whether or not the species was detected at least once during all counts at a given site within a given year.

When necessary, we adjusted these indices by using three variables that could influence bird detection but that were extraneous to the emphasis of the project (“extraneous variables” hereafter): observer identity (OBSX, analysed as a discrete variable); whether or not one could see beyond 100 m in all directions from the centre of a given site (VIS100, analysed as a discrete variable); and number of weekly bird counts used in analyses (NOWKS). The indices were adjusted by including these variables in regression models when the indices (dependent variables) were significantly related to the variables. Coding of discrete variables for regression analyses followed techniques described by Neter et al. (1989).

We used VIS100 to adjust the indices for local-scale conditions near the count site (e.g. vegetation density and height, abrupt topography) that could screen aural or visual cues, or in other ways influence bird detectability. Because of weather and logistical problems, a few sites did not get sampled during all 12 weeks of the study season. For analyses of the probability of occurrence, NOWKS was used to adjust for variation in the presence and absence of species associated with number of samples (weekly counts). NOWKS was not used as a covariate in analyses of species richness or relative abundance because our calculation of these indices already incorporated the number of counts for a given site.

Other approaches are available to adjust indices of species richness, occurrence, and abundance for species’ detection probabilities, but we did not use these techniques for several reasons. Adjustment of estimates of species richness based on capture-recapture methods (Boulinier et al., 1998; Hines et al., 1999; Cam et al., 2000) assumes that there is negligible change in the species that are actually present (the “population” of species is closed) from one sampling event to the next. Significant changes in species composition in BBNP during our sampling period (~10 species in March and ~20 species in each of the months of April and May; Wauer, 1996:7) clearly violate this assumption. To minimize the extent to which the closed-population assumption would be violated, we considered restricting our analysis to data from two or three consecutive (weekly) visits, but even within this time frame, the change in species composition in BBNP is not negligible. Furthermore, for many of the uncommon species we studied, we detected only one individual during 12 visits to a site during a given spring, and this occurred on many sites. With only two or three visits, some uncommon species that were present would probably not have been detected at all, which would have biased our estimates of richness. In addition, because of the flux in species composition, data for only two or three

visits would not adequately characterize the communities we studied during the spring.

A recent approach for adjusting species’ occurrence data based on patterns of detection and nondetection (MacKenzie et al., 2002) assumes that site occupancy does not change (population is closed) during the survey period. We could not make this assumption for a given site because in BBNP during our 12-week survey period, breeding migrant numbers change significantly with the chronology of migration (Wauer, 1996:7), and most of the residents and migrants involved in the present analysis produce young (Wauer, 1996:12–15). The closed population assumption can be met more easily by using only those data that are collected between the first and last date of a species’ detection, so that the species was present and capable of being detected during the whole of that part of the survey period (MacKenzie et al., 2002). This approach requires not only that the species be detected at a site at least twice (dates of first and last detections), but also that there be at least two (but preferably ≥ 5) sampling occasions between these two dates (MacKenzie et al., 2002).

Our research questions addressed landscape and community relations during the entire spring period, not part(s) of it, so using only part of the data would not have been appropriate. Reproduction (recruitment into the population) and initial dispersal could easily have violated the closure assumption as it relates to site occupancy, and attempts to circumvent its effects via data truncation (e.g. to exclude reproductive periods) would have exacerbated the problem of addressing only a small part of the spring season. If we had truncated our data, we also would have had to exclude species or sites from a given year’s analysis because of several circumstances we encountered for uncommon species: the species was either never detected, detected once, detected during only two consecutive sampling occasions (dates of first and last detection, which are not used in calculations involving truncated data; MacKenzie et al., 2002), or the number of sampling occasions between the dates of the first and last detection was only one. Valuable information about uncommon species would have been lost.

Double sampling (Bart and Earnst, 2002) can be used to adjust indices of abundance. This approach involves rapid sampling (e.g. point counts) of a large sample of sites, and intensive sampling (e.g. territory mapping) of a subset of the larger sample of sites. For some of the uncommon species involved in the present analysis, the 12 weekly 20-min counts yielded only one detection at a site during an entire season, indicating that with fewer sampling visits or shorter count periods, uncommon species may have gone completely undetected. To ensure the robustness of our inferences, it was important that we involve as many sites as possible, and our community-level focus required that we get indices of abundance or occurrence for as many species as possible, including

uncommon species. We did not have sufficient personnel to meet these sampling needs and at the same time conduct the intensive sampling needed for the double-sampling procedure. For the same reasons, we also did not have sufficient personnel to apply the double-observer method (Nichols et al., 2000) for adjusting abundance indices; furthermore, the double-observer approach does not work well for uncommon species (Thompson, 2002).

To use distance-sampling methods to adjust abundance indices, the number of detections for a species should “generally be at least 60–80,” and “although for some purposes, as few as 40 might be adequate,” typically, a number of detections “as small as 40 for an entire study is unlikely to achieve the desired precision” (Buckland et al., 1993:14). If estimates having a coefficient of variation = 0.15 are desired, for example, the number of detections needed per species often is 60–100 (Rosenstock et al., 2002). Within a given year, we did not have 60–100 detections for some of the uncommon species, and we chose not to risk using imprecise estimates of adjusted abundance that can result from analysing fewer detections.

Removal models (Farnsworth et al., 2002) can be used to adjust abundance estimates too, but they require that counts be short (e.g. 5 min) so that the assumption of a closed population during the count is less likely to be violated. Our use of 20-min counts was necessary to improve detection of uncommon species. It is quite possible, however, that during our 20-min counts the removal-model assumption of closure was not met, especially for wide-ranging species (Farnsworth et al., 2002).

In summary, we avoided potential biases associated with the production of aural and visual cues by controlling the daily and seasonal timing of our counts and conducting counts only during appropriate weather conditions. By avoiding the dawn chorus and noise from rain or wind, the daily timing of counts and our standards for weather conditions also enabled us to avoid potential biases related to detection of aural cues. Possible biases associated with aural and visual cue detection were avoided further by using relatively long (20-min) counts; sampling each site 12 times each year; employing experienced technicians and restricting their clothing colour; using a detection-recording protocol that prevented double counting but included birds that flushed or stopped vocalizing at the approach of the technician; and analytically adjusting richness, relative abundance, and probability of occurrence with techniques that did not require assumptions that were questionable or untenable for our data.

3.6. Model development

To control for environmental variation that was associated with our road and development variables, and to account for environmental variation that had the

potential to influence bird community structure, we included in regression analyses the elevation of the site and the percentages of the landscape within 2 km that were covered by igneous grassland, limestone grassland, and desert shrubland.

To avoid Type II errors, we used an a priori $\alpha = 0.10$ (instead of 0.05) for all analyses (Westmoreland and Best, 1985). Within a model for a given dependent variable, all of the hypotheses about whether there was a significant relation between the dependent variable and explanatory (road, development, environmental, and extraneous) variables were related because they all involved the same dependent variable. Hence, there was a family of simultaneous hypotheses (sensu Miller, 1981) to be tested for each dependent variable. To avoid Type I errors, we determined which explanatory variables were significantly associated with a dependent variable by applying a sequential Bonferroni adjustment to a family-wide $\alpha = 0.10$ (Rice, 1989).

Relations between species richness and explanatory variables, and relations between a species' relative abundance and explanatory variables, were assessed with stepwise least-squares regression (Proc Reg, SAS, 1989). Relative abundance was analysed only for species that were detected at $\geq 90\%$ of the 70 sites during a given study season. Species that were less abundant than this were absent at many sites, which caused the number of relative abundances equalling 0.0 to be too high for us to meet assumptions of least-squares regression.

When necessary, we applied a $\log_{10}(Y+1)$ transformation (Zar, 1999) to the dependent variable to normalize error-term distributions or stabilize error-term variances. Residual analyses confirmed that all regression assumptions (Neter et al., 1989) were met for each final model. We computed variance inflation factors, and all were ≤ 5.1 (mean = 1.5), indicating that regression coefficients did not have high variance due to correlation among explanatory variables in the model (Montgomery and Peck, 1982). Each final model had a significant overall F statistic and significant t statistics for coefficients associated with individual explanatory variables.

R^2 was used to report the percentage of variation in the dependent variable that was associated with the set of explanatory variables in a least-squares regression model (Neter et al., 1989). To validate these models, we used the prediction sum of squares to compute R^2 for prediction. This statistic describes a model's ability to predict each case correctly based on the model estimated from the remaining $n-1$ observations, and it measures the percentage of variation the model would account for if tested with comparable new observations. R^2 for prediction is commonly used to validate models when the sample size is not large enough for data splitting, or when additional test observations cannot be

obtained (Montgomery and Peck, 1982); both of these conditions applied to our analysis.

We used stepwise logistic regression (Hosmer and Lemeshow, 1989; Proc Logistic, SAS, 1989) to relate a species' presence or absence (hence probability of occurrence) to explanatory variables. When species were present on <20% or $\geq 90\%$ of the 70 sites, the problem of complete or quasi-complete separation (Hosmer and Lemeshow, 1989) occurred in some logistic-regression models. This problem can lead to questionable results (Hosmer and Lemeshow, 1989; SAS, 1989), so we used logistic regression only for species that occurred at least once on $\geq 20\%$ but <90% of the 70 sites. Species that were present on <20% of the sites were not studied separately with logistic regression but were included in richness analyses. For species analysed with logistic regression, non-zero relative abundances for a species were converted to the number 1 (species occurred); relative abundances of 0.0 were converted to the value 2 (species did not occur).

We identified the most appropriate logistic-regression model for each species based on several criteria: the -2 Log L statistic and the Score statistic for the model were significant, indicating that the explanatory variables as a group were significant (SAS, 1989); each explanatory variable had a significant -2 Log L statistic, which confirmed that each explanatory variable was individually significant (Allison, 1999); and to ensure that numerical problems such as complete or quasi-complete separation, zero cell counts, collinearity, and imprecise estimates of coefficients were not influential, explanatory variables whose coefficients had aberrantly large standard errors were not retained in the model (Hosmer and Lemeshow, 1989).

Max-rescaled R^2 was used to report the percentage of variation in the dependent variable that was associated with the set of explanatory variables in a logistic-regression model (Nagelkerke, 1991; SAS, 1996). To validate these models, we used Proc Logistic to determine the percentage of sites that a model correctly classified in terms of a species' occurrence. This percentage summarized a model's ability to predict each case correctly based on the model estimated from the remaining $n-1$ observations. For site classification, we used the conservative cut-off probability level of 0.5 and judged classification accuracy to be greater than chance accuracy when correct classification was at least 62.5% (Hair et al., 1998).

4. Results

4.1. Bird and landscape data

We detected 157 bird species during the three study seasons, but 67% (105) of these occurred on <10% of

the sites during most years (K.J. Gutzwiller, unpublished data); 26 species ("focal species" hereafter) were detected at $\geq 20\%$ of the 70 sites each year and were therefore abundant enough to study quantitatively. Magnitudes of most of the broad-scale road and development variables and environmental variables varied considerably among the 70 landscapes (Table 2). Thus, our data involved a wide range of road lengths at two spatial extents; a wide variety of spatial configurations among sites, roads, and development; and a wide range of environmental conditions.

4.2. Broad-scale road and development relations

Species richness, and relative abundance or probability of occurrence for 21 of the 26 focal species were significantly associated with road or development variables during one or more years (Table 3). Road or development variables were significant in 34 of the 81 analyses (27 dependent variables \times 3 years = 81), and environmental or extraneous variables were significant in 23 of those 34 analyses. Of the 81 analyses, 43 resulted in models that included environmental or extraneous variables but no road or development variables. No explanatory variables were significant in four of the 81 analyses. R^2 ranged from 6 to 73% for models with at least one road or development variable (including models with and without other explanatory variables), and from 6 to 28% for models with only road or development variables. R^2 for prediction was within 5 absolute % units of R^2 for the original model for four of the 22 least-squares models, and it was within 6–10 absolute % units of R^2 for the original model for 13 of the 22 models. Classification accuracy was higher than chance accuracy for 48 of the 55 logistic models, and the classification accuracy of these 48 models ranged from 63 to 89%.

Table 2
Summary statistics for road, development, and environmental variables^a

Variable and units	Mean	S.E.	Range
R1 (km)	2.11	0.08	0.31–5.34
R2 (km)	5.31	0.24	1.39–14.96
NR (km)	0.40	0.01	0.33–0.70
ND (km)	10.80	0.83	0.38–29.32
R1 \times R2 (km ²)	12.10	1.01	0.43–52.22
R1 \times NR (km ²)	0.83	0.04	0.22–2.38
R1 \times ND (km ²)	21.90	1.83	1.70–76.42
R2 \times NR (km ²)	2.09	0.09	0.98–5.98
R2 \times ND (km ²)	53.36	4.48	2.65–215.63
NR \times ND (km ²)	4.23	0.32	0.17–11.49
EL (m)	872.7	25.2	576–1574
IG (%)	29.6	3.3	0.0–95.5
LG (%)	15.5	2.7	0.0–100.0
DS (%)	43.6	3.0	0.0–93.8

^a $n = 70$; variable abbreviations and descriptions are in Table 1.

Table 3

Regression models relating species richness and relative abundance or probability of occurrence for 26 focal species to road, development, environmental, and extraneous variables, 1995–1997

Dependent variable	Regression coefficients, explanatory variables, and significance levels ^a	R ² (%)	Predictive ability (%)
Richness			
1995 ^{b,c}	0.90–0.002 (DS)***	12	8
1996 ^{b,c}	0.57+0.0002 (EL)***+0.10 (OBS1)****	28	21
1997 ^{b,c}	0.82–0.001 (R2×ND)****+0.0002 (EL)***+0.12 (OBS1)****	45	38
Turkey vulture (<i>Cathartes aura</i>) ^d			
1995 ^{b,c}	0.27–0.01 (NR×ND)**	6	1
1996 ^{b,c}	0.07+0.09 (R2×NR)****	15	2
1997 ^{b,c}	0.24+0.002 (DS)*–0.15 (OBS2)****	18	10
Scaled quail (<i>Callipepla squamata</i>)			
1995	–1.50+2.60 (OBS1)****+1.15 (OBS3)*	30	74
1996	–3.43+0.003 (EL)**+1.28 (OBS1)**	16	70
1997	–0.38–2.41 (R1×NR)**+0.004 (EL)***	22	70
White-winged dove (<i>Zenaida asiatica</i>)			
1995	4.34–0.03 (DS)**–0.004 (EL)***+1.05 (OBS1)*	27	73
1996	2.89–0.05 (R1×ND)**–0.003 (EL)**	13	64
1997	8.45–0.10 (IG)****–0.08 (LG)***–0.10 (DS)****–1.33 (VIS100)**	32	73
Mourning dove (<i>Zenaida macroura</i>)			
1995	1.01–0.03 (IG)***–0.02 (LG)*+1.28 (OBS1)**	24	63
1996	–0.24+1.34 (OBS1)**	10	61
1997 ^b	NS	NS	NS
Greater roadrunner (<i>Geococcyx californianus</i>)			
1995	2.95–0.24 (R2)*–0.03 (DS)**	14	69
1996	1.44–0.04 (R1×ND)*–1.71 (OBS2)***–1.89 (OBS3)***	25	67
1997	–1.89+0.004 (EL)**–2.76 (OBS3)****	26	74
Lesser nighthawk (<i>Chordeiles acutipennis</i>)			
1995	–3.27+0.08 (R1×ND)****	28	79
1996	–4.32+0.82 (R2×NR)**–0.05 (LG)***+3.82 (OBS1)****+2.91 (OBS2)****	43	80
1997	6.16–0.20 (ND)****+0.04 (DS)**–0.01 (EL)****–2.60 (OBS1)***	50	86
Ladder-backed woodpecker (<i>Picoides scalaris</i>)			
1995	–0.32–0.10 (IG)**–0.07 (LG)*–0.11 (DS)***+0.01 (EL)****–1.92 (VIS100)**	51	74
1996	0.27+0.02 (IG)*–0.03 (DS)**	27	60
1997	4.17–0.07 (R1×ND)***–0.91 (R2×NR)**–0.03 (DS)**	32	66
Say's phoebe (<i>Sayornis saya</i>)			
1995	0.43–0.19 (NR×ND)**	7	60
1996	0.73–0.86 (VIS100)*	6	61
1997	–0.44+0.02 (DS)*	6	63
Ash-throated flycatcher (<i>Myiarchus cinerascens</i>)			
1995	–2.34+0.01 (EL)**	14	89
1996 ^{b,c}	0.18–0.07 (R1×NR)**	6	1
1997 ^b	0.29+0.003 (LG)*+0.24 (OBS1)***	17	10
Loggerhead shrike (<i>Lanius ludovicianus</i>)			
1995	–1.43+0.03 (IG)****+1.42 (OBS1)**	22	69
1996	1.19–0.02 (LG)*	7	69
1997	0.88–0.02 (LG)**+1.72 (OBS2)**	17	73
Bell's vireo (<i>Vireo bellii</i>)			
1995	NS	NS	NS
1996	–2.18+0.24 (NR×ND)**	12	76
1997	1.03–1.18 (R1)**	10	80

(continued on next page)

Table 3 (continued)

Dependent variable	Regression coefficients, explanatory variables, and significance levels ^a	R ² (%)	Predictive ability (%)
Common raven (<i>Corvus corax</i>)			
1995	−2.79 + 0.42 (NOWKS)***	23	89
1996	NS	NS	NS
1997	2.32−0.03 (LG)**	11	83
Verdin (<i>Auriparus flaviceps</i>)			
1995	0.36 + 0.03 (LG)*	7	67
1996	1.68−0.01 (R2×ND)*	7	70
1997	1.68−1.03 (R1)** + 1.41 (OBS1)**	19	61
Cactus wren (<i>Campylorhynchus brunneicapillus</i>)			
1995 ^{b,c}	−0.17 + 0.001 (IG)** + 0.0004 (EL)****−0.10 (OBS3)***	49	42
1996	−3.38 + 0.01 (EL)***	20	84
1997 ^b	−0.72−0.67 (R1×NR)** + 0.003 (EL)****−0.49 (OBS3)**	37	28
Rock wren (<i>Salpinctes obsoletus</i>)			
1995	−1.84 + 0.10 (ND)** + 0.04 (IG)*** + 0.07 (LG)***	31	74
1996	−0.18 + 0.11 (IG)****	38	79
1997 ^{b,c}	0.34−0.002 (DS)**−0.08 (VIS100)**	15	7
Bewick's wren (<i>Thryomanes bewickii</i>)			
1995	−5.47 + 0.03 (LG)** + 0.01 (EL)****−1.23 (VIS100)**	35	77
1996	−13.17 + 0.04 (LG)** + 0.01 (EL)**** + 1.82 (OBS1)* + 3.90 (OBS3)****	71	81
1997	4.81−1.43 (R2×NR)**−0.06 (DS)****−2.07 (OBS2)** + 2.07 (OBS3)**	58	77
Black-tailed gnatcatcher (<i>Poliophtila melanura</i>)			
1995 ^b	0.88−0.01 (R1×R2)**−0.19 (OBS1)**	13	6
1996 ^{b,c}	0.24−0.004 (R1×R2)**	9	5
1997	3.63−0.03 (LG)**−1.67 (VIS100)**	21	89
Northern mockingbird (<i>Mimus polyglottos</i>)			
1995	−3.87 + 0.01 (EL)*** + 2.19 (OBS2)**	28	86
1996 ^{b,c}	−0.01 + 0.0002 (EL)****	16	8
1997 ^b	1.11−0.02 (R1×R2)** + 0.01 (IG)**** + 0.01 (LG)**−0.32 (OBS2)**	34	22
Canyon towhee (<i>Pipilo fuscus</i>)			
1995	−11.28 + 0.11 (R1×R2)** + 0.04 (IG)** + 0.01 (EL)****−2.32 (VIS100)**	66	83
1996	−8.11 + 0.01 (EL)****	41	79
1997	−8.69 + 0.04 (LG)*** + 0.01 (EL)****	51	81
Rufous-crowned sparrow (<i>Aimophila ruficeps</i>)			
1995	−2.87−0.05 (DS)*** + 0.01 (EL)***−1.52 (VIS100)**	58	77
1996	−11.97 + 0.81 (ND)**−2.86 (NR×ND)*** + 0.02 (EL)****	73	77
1997	−6.86−0.08 (DS)**** + 0.01 (EL)**** + 2.18 (OBS3)**	73	83
Black-throated sparrow (<i>Amphispiza bilineata</i>)			
1995 ^{b,c}	0.31−0.43 (NR)* + 0.002 (IG)*** + 0.003 (DS)**** + 0.08 (OBS3)**	32	18
1996 ^{b,c}	−0.06−0.01 (NR×ND)** + 0.004 (IG)**** + 0.003 (LG)*** + 0.005 (DS)**** + 0.07 (OBS3)**	35	22
1997 ^{b,c}	0.63−0.44 (R1×NR)**** + 0.01 (R1×ND)**** + 0.06 (R2×NR)**−0.06 (NR×ND)**** + 0.0002 (EL)** + 0.06 (OBS1)*	47	30
Pyrhuloxia (<i>Cardinalis sinuatus</i>)			
1995	−2.67 + 0.04 (R2×ND)*** + 0.05 (IG)*** + 0.03 (DS)*	34	81
1996	−11.49 + 2.88 (R1)*** + 0.01 (EL)****	41	87
1997 ^{b,c}	0.37−0.06 (R1)***−0.002 (LG)** + 0.11 (OBS1)***	24	16
Blue grosbeak (<i>Guiraca caerulea</i>)			
1995	−3.85 + 0.01 (EL)***−0.37 (NOWKS)** + 3.22 (OBS1)**** + 2.14 (OBS2)**	36	79
1996	−2.53 + 0.002 (EL)**	8	61
1997	−0.0002−0.02 (DS)** + 1.68 (OBS3)***	23	69

(continued on next page)

Table 3 (continued)

Dependent variable	Regression coefficients, explanatory variables, and significance levels ^a	<i>R</i> ² (%)	Predictive ability (%)
Brown-headed cowbird (<i>Molothrus ater</i>)			
1995	−1.47 + 0.02 (LG)**	9	77
1996	1.71–1.06 (R1)**	11	60
1997	1.90–1.30 (R1)***	13	66
Scott's oriole (<i>Icterus parisorum</i>)			
1995	3.01–0.02 (DS)*−1.68 (OBS3)**	19	80
1996	NS	NS	NS
1997	−2.09 + 0.01 (EL)**	13	89
House finch (<i>Carpodacus mexicanus</i>)			
1995 ^{b,c}	0.17 + 0.10 (OBS2)***	10	3
1996 ^{b,c}	0.37–0.002 (IG)***−0.002 (DS)**−0.10 (OBS2)***	21	11
1997 ^{b,c}	0.25–0.10 (R1×NR)*+0.002 (LG)**	14	7

^a Significance levels for explanatory variables (variable abbreviations are in Table 1 and Section 3) are: * $P \leq 0.10$, ** $P \leq 0.05$, *** $P \leq 0.01$, **** $P \leq 0.001$; NS indicates no significant relation between a dependent variable and explanatory variables.

^b Results for this dependent variable and year are based on least-squares regression for species richness or a species' relative abundance; results for dependent variables and years not marked with this letter are based on logistic regression involving a species' probability of occurrence. Under R^2 , standard R^2 is reported for least-squares models, and Max-rescaled R^2 is reported for logistic models. Under predictive ability, R^2 for prediction is given for least-squares models, and the correct classification percentage is given for logistic models.

^c $\log_{10}(Y+1)$ transformation was applied to the dependent variable.

^d All common and scientific names of birds are from American Ornithologists' Union (1998).

4.3. Complexity of broad-scale road and development relations

Of the 34 models involving road and development variables, 31 reflected relations between the dependent variable and explanatory variables that were non-linear (least-squares models involving a \log_{10} transformation, or logistic models; Table 3). Interactions involving total road length within the 1- and 2-km extents, distance to the nearest road, or distance to the nearest development (primarily R1×NR, R1×ND, R2×NR, and NR×ND) were significant in 23 of the 34 models; simple main effects (primarily R1 and ND) were significant in 11 of the 34 models. As main effects and components of interaction effects, the total lengths of roads within the 1- and 2-km extents were significant in 26 of the 34 models. Within each of the 27 dependent variables, substantial interannual variation in the effects of roads and development was evident from the minimal among-year consistency in the variables that were significant.

5. Discussion

5.1. Broad-scale road and development relations

Our R^2 for prediction values indicate that most of the least-squares models for species richness and relative abundance were valid when tested with new data. R^2 for prediction will always be smaller than R^2 , but as long as

R^2 for prediction is within several absolute % units of R^2 , the original model does not depend greatly on a small number of observations and is therefore considered to have general applicability (Montgomery and Peck, 1982). R^2 for prediction values that differ substantially from R^2 suggest that a relatively small set of observations had important effects on model fit and that the model may be more applicable to the specific sample studied (e.g. our 70 sites) than it is to the general circumstances in question (e.g. BBNP). Although most of the least-squares models had general applicability, some of them had relatively low R^2 s and therefore limited practical value for prediction.

Max-rescaled R^2 values were often relatively low or moderate in magnitude, although for a few models with road or development variables, Max-rescaled R^2 was 50–73%. For most logistic models, the correct-classification percentages were higher than the chance-accuracy percentage, indicating that even models with low or moderate Max-rescaled R^2 s were valid when tested with new data. Thus, many logistic models had practical predictive utility despite their modest Max-rescaled R^2 values.

Our models apply to sites that were from 0.33 to 0.70 km from the nearest road. This range of distances resulted in part from efforts to minimize traffic noise and to maximize sample size (number of sites) and sampling intensity (number of visits per site). Noise from traffic can reduce the density of breeding birds near roads (e.g. Reijnen et al., 1995). Traffic noise did

not hamper bird sampling at the distances involved in our study, but it is possible that noise effects may be responsible for the positive relations we observed between some bird metrics and NR (Table 3). Noise effects may be more significant at sites that are <0.33 km from roads in BBNP, but our models cannot be used to draw inferences about this possibility because these distances lie outside of the range of NR involved in our analyses.

Our results establish that general road and development influences are important enough in BBNP that more detailed studies of effects of road type and development type are warranted. As a first step, effects of paved and unpaved roads with different widths, traffic volumes and speeds, and proximity to trails should be studied. Effects of different types of development (e.g. visitor centres, trailer parks, gas stations) on nearby bird community structure also should be analysed. Such assessments represent natural follow-up analyses of our initial study; similar evaluations may be valuable in other protected areas.

5.2. Complexity of broad-scale road and development relations

Complexity in the form of non-linear relations, interaction effects, spatial-extent effects, and interannual variation was common for the bird–landscape associations we observed, indicating that simple linear models derived for a single spatial extent or year would not adequately characterize road and development effects in the landscapes we studied. Interaction effects represent complex influences that cannot be managed via strategies based on main (additive) effects. Knowledge of interaction effects of roads and development on birds remains limited because conservationists have not typically tested for such influences.

The interaction effects we studied (Table 1) are known in the context of regression as “moderator effects” (Hair et al., 1998). A moderator effect occurs when the slope of the relation between the dependent variable and one explanatory variable varies with the values of another explanatory variable—the moderator variable (Hair et al., 1998). For example, if $NR \times ND$ was significant, the effect of NR on the dependent variable varied with (was moderated by) ND or, alternatively (Neter et al., 1989), the effect of ND varied with NR. In the absence of interaction effects, the slope of the relation between the dependent variable and an explanatory variable does not differ across levels of another explanatory variable.

Within species, the interannual variation we observed among models was not due to changes in road length or development because the amounts and locations of these factors did not change appreciably during, or for several to many years before, our study (see Section 2). We recommend that conservationists routinely assess

whether the complexity we observed characterizes relations between bird metrics and roads or development because knowledge of complex associations, not just simple ones, is needed to improve ecological understanding and conservation effectiveness.

5.3. Bird community structure

Environmental and extraneous variables were important in many of the models, and by controlling analytically for their effects, we were able to develop a clearer view of the influence (or lack of influence) of roads and development on bird community structure than we would have if we had not accounted for these variables. The focal species were the primary constituents of the communities we studied, and species richness as well as the relative abundance and probability of occurrence of most of these species were significantly associated with road or development variables, even after we controlled for environmental and extraneous variables. These results imply that broad-scale road and development variables had important effects on bird community structure in our system.

Our low and moderate R^2 values, which are similar in magnitude to those reported for other bird–landscape models (e.g. Lynch and Whigham, 1984; Askins et al., 1987), imply that although roads and development had significant effects, they represent only two of the factors that influence bird community structure in BBNP. Our models indicate that some of the variation in the bird metrics was related to local-scale variables (VIS100, EL) and broad-scale variables (IG, LG, DS). The latter three variables reflected vegetative coverage of the landscape by particular floristic compositions (see Section 2) and their associated physiognomic structures. The remaining variation may have been associated with finer- or coarser-scale factors including, for example, food density, available nest sites, proximity to other natural areas, or regional population sizes. Because our emphasis here was on effects of broad-scale road and development variables, an examination of numerous other finer- and broader-scale factors was beyond the scope of our research.

5.4. Implications for protected areas

To the extent that a large natural area serves as an important source of indigenous bird communities in a region, roads and development may have repercussions on bird community conservation not just within the natural area, but also far beyond its boundaries. Such off-site impacts were not the focus of the present study, but they deserve serious attention by conservationists. If roads and development within a park degrade native communities through changes in species composition or reduction in population sizes, the chance that native

communities in adjoining areas will be maintained by dispersal of indigenous species from the park may decline. Accordingly, it is imperative that conservationists understand the positive and negative effects of roads and development within parks, refuges, and other reserves. As we have demonstrated for BBNP, bird communities can be affected significantly even when road and development densities are relatively low.

Each protected area is likely to have unique internal and external environments, so it is improbable that relations and management approaches that are relevant for one reserve will be entirely appropriate for another. Our results apply to an arid protected area with relatively low magnitudes of road width, road density, traffic volume, and development density (see [Section 2](#)), and they may not apply to mesic or other natural areas with higher road or development disturbance. In short, it may often be necessary to conduct area-specific analyses and to develop area-specific management approaches.

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