
Biophysical Factors, Land Use, and Species Viability in and around Nature Reserves

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Abstract: *Many nature reserves are located in landscapes with extreme biophysical conditions. We examined the effects of interactions between biophysical factors and land use on bird population viability inside and outside of Yellowstone National Park. Our hypotheses were as follows: (1) biophysical factors constrain bird species richness and bird reproduction at higher elevations; (2) nature reserves are located at higher elevations, whereas private lands and more intense land use occur mostly at lower elevations with more mild climates and fertile soils; and (3) intense land use at lower elevations favors nest predators and brood parasites and thereby reduces reproductive output for some bird species. We used simulation models to evaluate whether favorable habitats outside reserves are population source areas and whether intense land use can convert these habitats to population sinks and reduce population viability within reserves. Bird species richness and abundance were high in small hotspots in productive, low-elevation habitats. Length of breeding season—and opportunity for renesting—was greatest at the lowest elevations for both American Robins (*Turdus migratorius*) and Yellow Warblers (*Dendroica petechia*). Nature reserves were higher in elevation than private lands, so hotspots for bird richness and abundance occurred primarily on or near private lands, where rural residential development was concentrated. Brown-headed Cowbirds (*Molothrus ater*) were significantly more abundant near rural homes, but nests of American Robins were not parasitized and their nest success did not differ with home density. Nests of Yellow Warblers were commonly parasitized by cowbirds, and their nest success was significantly lower near rural homes. Estimated intrinsic population growth (λ) for American Robins suggested that low-elevation hotspots were population source areas for this species. Estimated λ for the Yellow Warbler suggested that the entire study area was a population sink, likely due to the effects of intense land use at lower elevations and climate constraints at higher elevations. Removing the effect of land use from the simulations revealed that high-elevation hotspots were population sinks, whereas low-elevation hotspots were source areas. Our results are consistent with the possibility that bird-population source areas outside nature reserves can be converted to population sinks by intense human use, thereby reducing the viability of subpopulations within reserves.*

Factores Biofísicos, Uso de Suelo y Viabilidad de Especies en Reservas Naturales y sus Alrededores

Resumen: *Muchas reservas naturales se encuentran en paisajes con condiciones biofísicas relativamente extremas. Examinamos las interacciones entre los factores biofísicos y el uso del suelo en cuanto a la viabilidad poblacional de aves dentro y fuera del Parque Nacional Yellowstone. Nuestras hipótesis fueron las siguientes: (1) los factores biofísicos limitan la riqueza y la reproducción de especies de aves en alturas mayores; (2) las reservas naturales están a mayores alturas, mientras que los terrenos privados y los usos más intensos del suelo están principalmente a menores alturas con climas más templados y tierras más fértiles y (3) el uso intensivo de suelo a menores alturas favorece a depredadores y parásitos de nidos y, por lo tanto, reduce el éxito reproductivo de algunas especies de aves. Utilizamos modelos de simulación para evaluar si los hábitat favorables fuera de las reservas son áreas fuente para las poblaciones y si el uso intensivo de suelo puede convertir a esos hábitat vertederos y reducir la viabilidad poblacional dentro de las reservas. La riqueza y abundancia de especies fueron altas en pequeñas áreas en hábitat productivos situados a elevaciones bajas. La duración de la época reproductiva (y la oportunidad para volver a anidar) fue mayor a menores elevaciones para petirrojos (*Turdus migratorius*) y chipes amarillos (*Dendroica petechia*). Las reservas naturales estuvieron a mayor altura*

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que las tierras privadas; por lo tanto, las áreas de importancia para la riqueza y abundancia de aves principalmente se encontraron dentro de terrenos privados o cerca de los mismos, donde se concentró el desarrollo residencial rural. *Molothrus ater* fue significativamente más abundante cerca de las casas rurales; sin embargo los nidos de petirrojos no fueron parasitados y los nidos exitosos no difirieron con la densidad de casas. Los nidos de chipe amarillo comúnmente fueron parasitados por *M. ater* y los nidos exitosos fueron significativamente menos cerca de las casas rurales. El crecimiento poblacional intrínseco (λ) estimado para petirrojos sugirió que los sitios de importancia en elevaciones bajas fueron áreas fuente para esta especie. La λ estimada para los chipes amarillos sugiere que toda el área de estudio fue un vertedero para la población, probablemente debido a los efectos del uso intensivo del suelo y las restricciones climáticas a mayores alturas. La exclusión del efecto del uso del suelo de las simulaciones indicó que las áreas de importancia a mayores alturas eran vertederos, mientras que las de áreas bajas eran fuentes. Nuestros resultados son consistentes con la posibilidad de que las áreas fuente de poblaciones de aves por fuera de las reservas naturales pueda convertirse en vertederos por el uso humano intensivos, reduciendo por lo tanto, la viabilidad de sub poblaciones dentro de las reservas.

Introduction

Nature reserves are a cornerstone of strategies for conserving biodiversity, but native species are going extinct even in reserves (Newmark 1987a, 1987b, 1996; Woodroffe & Ginsberg 1998). These extinctions generally have been attributed to the small size and isolation of nature reserves (Wilcove & May 1986; U.S. General Accounting Office 1994). The effectiveness of reserves has also been questioned because their location is perceived to be nonrandom (Hansen & Rotella 2001). Nature reserves are disproportionately located at higher elevations and on less fertile soils, whereas the most productive landscapes occur largely on private lands (Hunter & Yonzon 1993; Scott et al. 2001). Because of these patterns of land allocation, habitat destruction through deforestation and agriculture has been concentrated on productive sites in lowland, coastal, and riparian areas (Huston 1993; Laurance et al. 1999). The implications of the nonrandom location of nature reserves and protected habitats for biodiversity are poorly understood. The topic is especially germane now because the remaining wild and semiwild habitats around many reserves are rapidly being claimed for intense human use, functionally increasing the biased location of natural habitats (Newmark 1996; Hansen & Rotella 2001).

Reserves located in especially cold, dry, or unfertile landscape settings (termed unfavorable landscape settings) may not be sufficient for protecting the biodiversity within them. Species within such reserves may also require more-favorable landscape settings with more moderate climate, fertile soils, and available water outside of the reserve. Because favorable landscape settings have often been claimed as private lands, land use may be intense in these settings. Thus, the negative influences of intense land use on biodiversity in favorable landscape settings outside of reserves may reduce the viability of native species within nearby reserves.

We speculate that the interactive effects of biophysical factors and land use can lead to complex population dynamics for some species. Subpopulations of a species within a reserve may suffer increased risk of extinction if population source areas outside the reserve are degraded by human activities (Sinclair 1998). Population sources are areas where births exceed deaths and the finite rate of population increase (λ) exceeds the replacement level of 1 (Pulliam 1988). Subpopulations may persist in sink habitats ($\lambda < 1$) if they receive sufficient immigration from source habitats ($\lambda > 1$) (Pulliam & Danielson 1991). We suggest that the harshness of physical factors in reserves may result in populations within nature reserves being dependent upon population source areas in more-favorable settings outside of reserves. As the more-favorable landscapes surrounding nature reserves are altered by human activities, population source areas may be converted to population sinks, thereby increasing the risk of extinction within reserves.

We examined interactions among biophysical factors, human land allocation and use, and the population attributes of bird species in the Greater Yellowstone Ecosystem. Hypotheses evaluated were as follows: (1) at higher elevations, biophysical factors constrain bird species richness, bird abundance, length of nesting season, and reproductive output, whereas at lower elevations, these factors are less constraining; (2) human land allocation and use has resulted in nature reserves being placed at higher elevations, whereas private lands and more-intense land use are at lower elevations with milder climates and more-fertile soils; (3) intense land use favors nest predators and brood parasites and thereby reduces reproductive output for some native species. If these hypotheses are correct, a potential consequence is that intense land use at lower elevations could convert population sources to sinks and increase the risk of extinction of subpopulations in nature reserves at higher elevations.

We tested these hypotheses with field studies. We

then examined potential population consequences using simulation modeling of population growth rate and statistical extrapolation of source-sink status across landscapes. We focused on the reproduction and population growth of two species, the American Robin (*Turdus migratorius*) and Yellow Warbler (*Dendroica petechia*), that were expected to differ in response to land use because of their respective life-history attributes. For the Yellow Warbler, which was predicted to be sensitive to land use, we also evaluated the possibility that land use in population source areas outside reserves could reduce population viability in reserves.

Methods

Study Area

The 9500-km² study area included the upper Gallatin, Madison, and Henry's Fork watersheds in Montana, Idaho, and Wyoming (U.S.A.) (Fig. 1). These rivers originate on a plateau in Yellowstone National Park, pass through the Gallatin and Targhee national forests, and flow into privately owned agricultural floodplains in the lowlands.

Climate severity and soil quality varied with elevation in the study area. Mean annual temperature and growing-degree days varied from 5.8° C and 2787 days below 1500 m to 0.26° C and 1356 days above 2400 m during 1995–1997 (Hansen et al. 2000). Much of the precipitation fell as snow. Average snowmelt date during this period was 1 May at 1500 m and 1 July at 2400 m. The Yellowstone Plateau was created through volcanic activity. Hence, soils at higher elevations are largely nutrient-poor rhyolites and andesites with low water-holding capacity (Rodman et al. 1996). Valley bottoms and floodplains contain glacial outwash and alluvium soils that are higher in nutrients and water-holding capacity.

The vegetation of the study area was a mosaic of forests, shrublands, and grasslands (Despain 1990). Upland rhyolitic soils supported conifer forests. Sagebrush shrublands occurred on dry, fine-textured soils from low to middle elevations. Grasslands existed on fine-textured soils from valley bottoms up to middle slopes. Aspen (*Populus tremuloides*) was distributed in relatively small patches, primarily on moist toeslopes or on fractured rocks. Larger floodplains were dominated by black cottonwood (*Populus trichocarpa*) and narrowleaf cottonwood (*P. angustifolia*). Aboveground net primary productivity was related to elevation, soils, and cover type in the study area. It varied from 2964 kg/ha/year in subalpine conifer forests to 5508 in low-elevation, cottonwood forests (Hansen et al. 2000). Agriculture, range, rural-residential, and urban development were common land-use types on these private lands in the study area.

Bird Abundance, Richness, and Reproduction

We sampled abundances of landbirds on 100 sites stratified by cover type, seral stage, and elevation class during the breeding seasons of 1995–1997. Cover types included aspen, cottonwood, Douglas-fir (*Pseudotsuga menziesii*), grassland, sagebrush, and lodgepole pine (*Pinus contorta*), which were the major cover types of the study area below the alpine zone. We sampled in each of three seral stages of lodgepole pine: after recent fire, after recent logging, and mature and old growth. Elevation classes were <2200 m, 2200–2400 m, and >2400 m. Four to eight replicates were sampled per stratum. Sampling locations were located by inspection based on cover type, elevation class, geographic distribution, and access. We placed sampling sites widely over the study area to maximize the range of topographic, climatic, and soil settings, but we constrained sites to those within 1.5 km of a road to facilitate access. At each site, birds were counted on six 100-m radius points spaced >200 m apart by the fixed-plot method (Ralph et al. 1993). Two bird surveys were conducted during the 1995 breeding season, and three surveys were conducted each year in 1996 and 1997. The dates of the surveys varied with elevation to correspond to the height of bird breeding activity in each elevation class.

Elevation of sites was derived from digital elevation models and parent material from soil atlases. We estimated aboveground net primary productivity for each point, based on tree and shrub density and annual diameter growth, using dimension analysis (Hansen et al. 2000). We estimated bird density by correcting counts for detectability with the program DISTANCE (Buckland et al. 1993). Bird abundance, aboveground net primary productivity, elevation, and parent material were averaged for each site, and site was used as the unit of analysis.

Relationships between predictor variables (cover type, elevation, parent material, and estimated aboveground net primary productivity) and bird abundance and richness were quantified by multiple regression. Competing regression models were analyzed, best models were selected based on Akaike's information criterion (AIC) and parsimony (Burnham & Anderson 1998), and best models were then used to predict bird species richness and abundances over the study area. These projections were not validated against independent data, but the coefficient of variation of the predictions was quantified as a measure of the confidence that could be placed in the results. We report results for bird species richness, total bird abundances, and abundances of the American Robin and Yellow Warbler.

Bird reproduction was estimated within two deciduous forest-cover types that differed in elevation: five cottonwood sites at 1000–1500 m and four aspen sites at 2000–2500 m. The two cover types also differed in land-use intensity. Cottonwood stands were on floodplains and were surrounded by rural residential development.

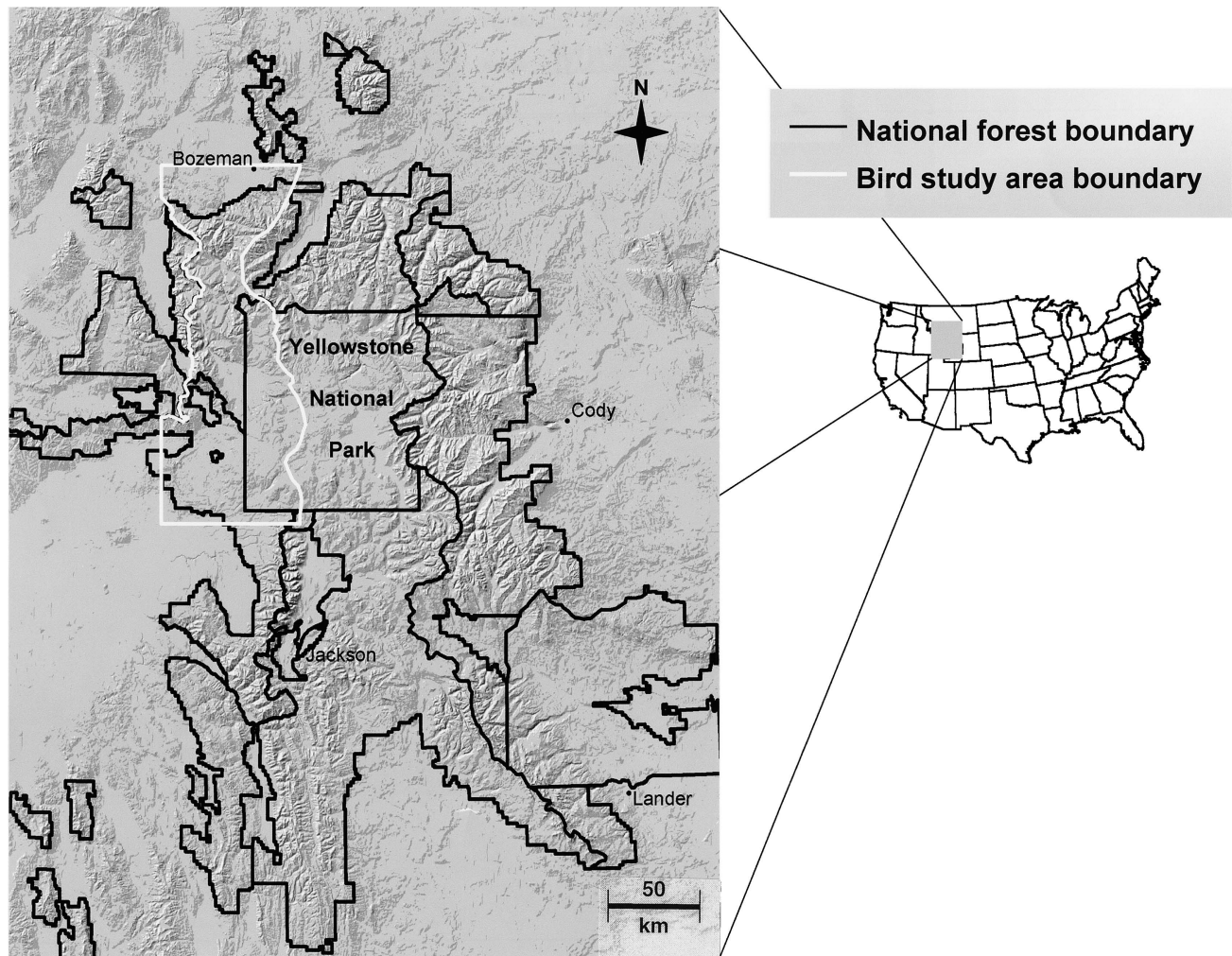


Figure 1. Location of the study area in the Greater Yellowstone Ecosystem.

Aspen stands occurred primarily on mountain-toe slopes and were distant from rural homes. On each site, we located and monitored the fates of nests (Martin & Geupel 1993) of several species during 1997–1999. Two bird species were selected for analysis based on adequacy of sample sizes and reported differences in their susceptibility to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), a bird associated with intense land use (Askins 1995). The species selected were the American Robin (never successfully parasitized) and the Yellow Warbler (commonly parasitized) (Ehrlich et al. 1988). American Robins also aggressively defend their nests and may be less vulnerable to predators than Yellow Warblers.

We searched for nests on each site every other day from mid-May through July. Each nest's contents and fate were monitored every 2 to 4 days until the nest failed or fledged young. For each nest, we recorded the number of eggs and young (host and cowbird) present during each visit and used these data to estimate production of eggs and young. Based on observed clutch sizes and dates for egg laying, hatching, and/or fledging of young, we estimated dates of

initiation, hatching, and fledging for each nest. These data were then used to estimate and compare the distribution of initiation dates and the length of the nesting season in each cover type. Using *t* tests, we compared the range of nest-initiation dates on each site between cover types for each species. Data from nests that survived through the egg-laying stage were used to calculate the cowbird parasitism rate for each species in each cover type.

We used generalized linear models and data on nest fates and covariates of interest (Rotella et al. 2000) to estimate the daily survival rates of nests. This maximum-likelihood analysis is an extension of Mayfield's (1975) approach to estimating nesting success, which makes the same assumptions as traditionally applied methods. We evaluated the strength of relationships between nest fate and covariates of interest, such as nesting stage and cover type, with Akaike's information criterion and the principle of parsimony (Burnham & Anderson 1998). Estimates of daily survival rate from the most parsimonious model for each species were used to generate estimates of nesting success (i.e., daily survival rate was raised to a

power corresponding to the number of days required to lay, incubate, and fledge young in the species).

Human Land Allocation and Use

As a measure of the allocation of lands relative to biophysical factors, we quantified the distributions of nature reserves, other public lands, and private lands across elevation. Included in the nature reserves were designated national parks, wilderness areas, and national wildlife refuges. Data on the boundaries of these land jurisdictions were obtained from the Montana State Library Natural Resource Information System.

Human population growth in the Greater Yellowstone Ecosystem has resulted in a rapid expansion of rural residential development (Hansen et al., 2002). Maps of home location were not available for the study area. County well records, recorded to a spatial accuracy of the quarter section, provided the best indication of home location. We assumed for this analysis that homes were built on locations where well permits had been granted, but the accuracy of this assumption could not be quantified fully. The actual locations of a subset of homes were known for about 20% of the study area. We found that the geographic distribution of the known home locations corresponded closely with the well-permit locations. The distribution of homes relative to bird hotspots was quantified by comparing the density of homes within 2 km of bird hotspots to the average density of homes across the private lands in the study area.

Land Use and Bird Reproduction

To evaluate whether land use negatively affected reproductive output, we compared various productivity measures between nests found in stands of aspen (low land-use intensity) and cottonwood (high land-use intensity). For the Yellow Warbler, we evaluated whether the probability of cowbird parasitism differed between cover types with a chi-square test. To evaluate whether nest survival differed between cover types for the American Robin and the Yellow Warbler, we used generalized linear models. For nests that did survive, we compared the number of young fledged per nest between cover types for each species with a *t* test.

Interactive Effects of Biophysical Factors and Land Use on Net Population Growth

To investigate potential population consequences of observed spatial patterns of species density and reproductive output, we estimated population growth rate (λ) for the American Robin and Yellow Warbler. We estimated λ for each species and cover type based on relevant estimates for simulated female success (proportion of females that successfully nested when potential renesting

was considered), field estimates of females fledged per successful nest, and published estimates of adult and juvenile survival rate. To calculate λ , we used Pulliam's (1988) equation: $\lambda = (\text{annual survival rate for adults}) + (\text{survival rate for juveniles}) \times (\text{number of females produced per female per year})$. We believe that this modeling strategy and structure represents a reasonable trade-off between simplicity and complexity (Levins 1966; Johnson 1996), given our objectives and the limited data on survival available for parameterizing the model. We considered the model adequately complex to further our understanding of the population dynamics of the species and for gaining information about the relative importance of different habitat settings. Given the simplifications and assumptions made, however, we recommend against using estimates of λ for predicting actual future population sizes.

We estimated female success with a stochastic model that incorporated field estimates of nesting success, average age of failed nests, and duration of the nest-initiation period by cover type. For each species and cover type, we used relevant field data and Monte Carlo simulations to estimate renesting potential and then combined renesting potential and nesting success to calculate female success. To estimate renesting potential, we (1) generated a distribution of initiation dates for 1000 initial nest attempts and all subsequent renest attempts for simulated females who repeatedly failed at nesting and (2) used that distribution to estimate the proportion of first, second, and third nesting attempts that fail in time to allow for a subsequent nesting attempt. To do this, we (1) generated a random initiation date for each female's first nest initiation (normally distributed based on observed data for the first 2 weeks of the nesting season, bounded by observed dates); (2) generated a random fail date for each nest (normally distributed according to observed survival times for all failed nests and bounded by observed nest ages at failure); (3) determined whether each nest failed in time to allow for another attempt (initiation date plus fail age plus 6 days of recovery time [Holcomb 1974]) before the end of the nesting season; and (4) repeated steps 1–3 (for a maximum of three renesting attempts) for females who failed and recovered in time for another nest attempt. Thus, female success was nesting success adjusted for up to three renest attempts and did not allow for multiple broods (the roles of third and fourth nesting attempts were modest in all habitat settings).

For each cover type and species, we multiplied simulated female success by the number of female young fledged per successful nest (a 50:50 sex ratio of young in each nest was assumed) to estimate the number of females fledged per female. Population growth rate was then calculated as described above, based on published estimates of survival. Because no estimates of survival were available for our area and rigorous estimates are

Table 1. Results of regression analysis of relationships between bird variables and biophysical factors (data from 100 stands distributed across the study area).

Variable	Significant models (R^2)	Best model			
		model	F	R^2	$p > F$
Species richness	elevation (0.19) parent material (0.41) ANPP* (0.56) cover type (0.64)	cover type, elevation, parent material	19.0	0.73	0.0001
Total abundance	elevation (0.29) parent material (0.27) ANPP (0.40) cover type (0.61)	cover type, elevation, parent material	20.0	0.70	0.0001
American Robin	elevation (0.16) parent material (0.18) ANPP (0.33) cover type (0.26)	cover type, elevation, parent material	4.0	0.34	0.0001
Yellow Warbler	elevation (0.45) parent material (0.48) ANPP (0.62) cover type (0.76)	cover type, elevation	19.5	0.81	0.0001

*Aboveground net primary productivity.

rare for the species we studied, we reviewed available estimates (Roberts 1971; Ricklefs 1973; Karr et al. 1990; Martin & Li 1992), summarized data, and used 0.6 and 0.5 for adult and juvenile survival in both species. These rates are typical of those reported for the two species and their close relatives. This method of dealing with the lack of survival data and the equation used to estimate λ are both commonly used in avian demographic studies, especially for passerines (e.g., Brawn & Robinson 1996; Fauth 2001; Flaspohler et al. 2001).

We projected the net population growth of Yellow Warblers over the study area with and without the influence of rural residential development. Net population growth was modeled across the study area by 100-m elevation class as a function of the predicted abundance of breeding females (as derived with the regression function in Table 1) and predicted λ (derived as described above). To calculate λ for each elevation class under the current land-use scenario, we first estimated nesting success and female success for each elevation class and then used these values in the equation for calculating λ . We estimated nesting success for each elevation class through an estimating model that included as a predictor variable the density of homes within 6 km of a site (see results for additional model details). For each elevation class we used the estimates of nesting success and potential renesting relevant to that elevation class to calculate female success. We removed the estimated effect of homes in a second analysis of predicted net population growth by setting the density of homes to zero when predicting nesting success at each elevation.

Under each scenario, we first calculated the abundance and net change in abundance for each elevation class and then summed across all elevation classes to estimate the net change in population size across all classes. This method assumes that the species disperses among suitable habitats in the study area such that source habitats exchange individuals with sink habitats. This assumption seems plausible given the territorial nature of passerines, the large number of studies that have reported sequential habitat occupancy (reviewed by Newton 1998), and the number of passerine species that have been

shown to regularly recolonize unoccupied suitable habitat (e.g., Opdam et al. 1995).

Results

Distribution of Bird Richness, Abundance, and Reproduction

Bird species richness, total bird abundance, and American Robin and Yellow Warbler abundances were positively associated with landscape settings that were lower in elevation, on alluvial parent materials, and/or had higher aboveground net primary productivity (Table 1). These sites were dominated by the deciduous forest-cover types of aspen, cottonwood, and willow. Extrapolating species richness and total bird abundance across the study area revealed that places predicted to have $\geq 60\%$ of maximum richness and bird abundance were relatively rare (Fig. 2). These hotspots covered only 2.7% of the study area and occurred primarily at lower elevations. Yellow Warblers were largely restricted to these hotspots, and American Robins were significantly more abundant in hotspots. Confidence in the predicted distribution of hotspots was bolstered by the low coefficients of variation of predicted bird richness and abundance. For species richness and total abundance in deciduous habitats, which were generally classified as hotspots, mean coefficients of variation were 0.087 (SD = 0.030) and 0.089 (SD = 0.021), respectively.

We obtained reproductive data from 441 American Robin and 340 Yellow Warbler nests. The nesting season was longer at lower elevations for both American Robins ($p = 0.02$) and Yellow Warblers ($p < 0.01$) (Table 2). At lower elevations, the nest-initiation period was extended by 14 days (SE = 4.4 days) for robins and 22.7 days (SE = 4.5 days) for warblers. Thus, there was significantly more time for renesting attempts by each species in cottonwood stands than in aspen stands. Other measures of reproductive output were not greater at lower

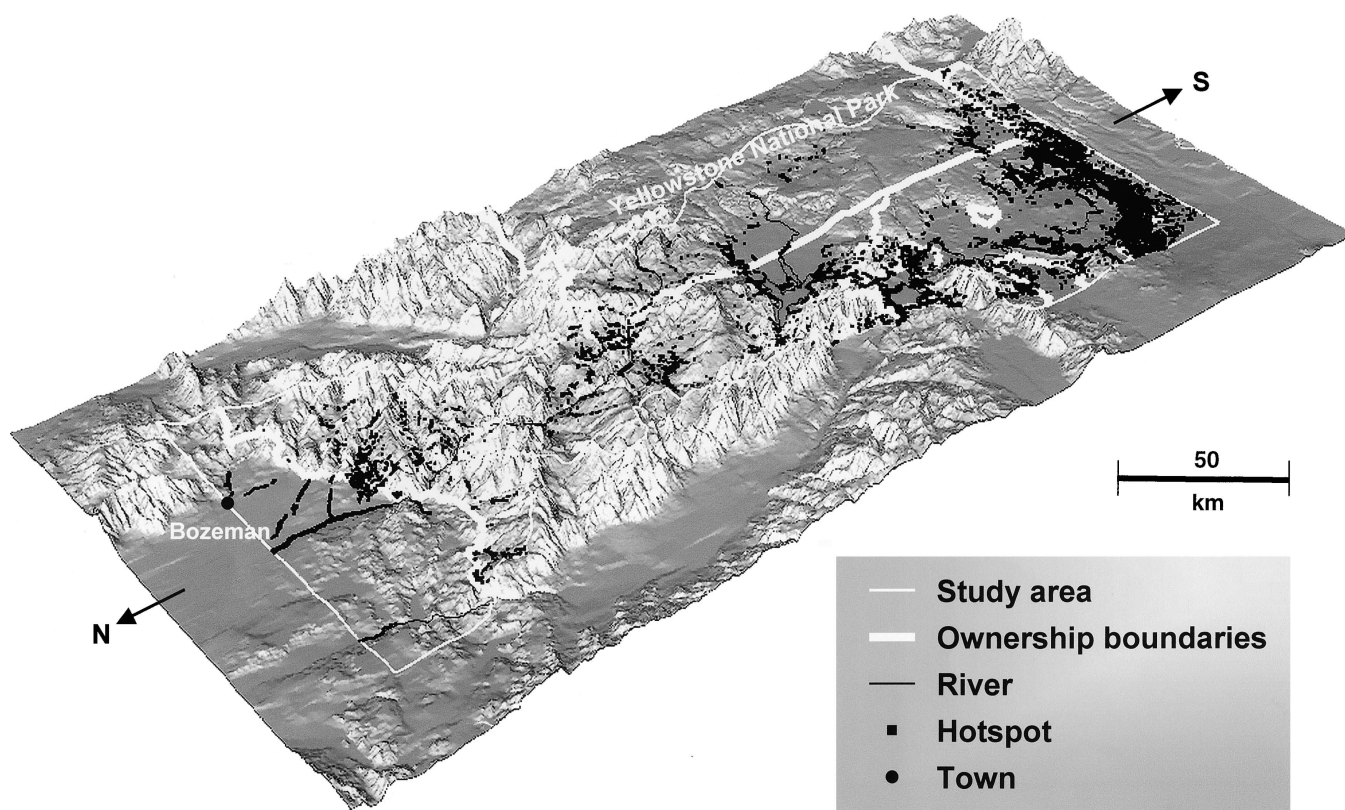


Figure 2. Distribution of bird hotspots (bird species richness and total abundance $\geq 60\%$ of maximum) across the study area (YNP, Yellowstone National Park; TNF, Targee National Forest; GNF, Gallatin National Forest).

elevations, which may be explained by the more intense land use associated with lower-elevation sites.

Distribution of Human Land Use

Human impacts on natural habitats in the study area were not random relative to biophysical gradients. The elevational range of reserves was higher (1700–3400 m) than that of private lands (1200–2600 m) (Fig. 3). The majority of the areas high in aboveground net primary productivity (> 4500 kg/ha/year) occurred on private lands; only 1.0% of these areas occurred in nature reserves (Hansen et al. 2000). Consequently, hotspots for bird richness and abundance occurred primarily on or near private lands. Sixty-seven percent of hotspots were found on or within 6 km of private lands, whereas only 6.5% were found in nature reserves. Within private lands, rural residential development was placed disproportionately close to bird hotspots. Home densities within 2 km of hotspots were 67% higher than at random locations on private lands.

Effects of Land Use on Reproduction

Lower-elevation sites had more intense land use and greater densities of brood parasites and avian predators.

The density of homes within 6 km of cottonwood stands (986/ha, SE = 70.2) was higher than that around aspen stands (153/ha, SE = 38.7). Cowbird density was positively related to home density within 6 km of a site ($n = 11$, $F = 64.7$, $R^2 = 0.89$, $p < 0.0001$) and was higher in stands of cottonwood (2.58/ha, SE = 0.13) than in aspen (0.70/ha, SE = 0.03). Similarly, the abundance of the avian nest-predator guild was also positively associated with home density ($n = 11$, $F = 32.3$, $R^2 = 0.78$, $p < 0.0003$). We were unable to determine the proportion of nest failures due to nest predation but did quantify the proportion of nests that were parasitized. No American Robin nests contained cowbird eggs. In contrast, Yellow Warbler nests were commonly parasitized, and the rate was 5.1 times greater ($p < 0.001$) in cottonwood (44.2%) than in aspen stands (8.7%).

For American Robins, which were regularly seen chasing brood parasites and avian predators on our sites, nesting success did not appear to differ between cover types. For robins, a model that estimated a common daily survival rate for aspen and cottonwood stands was slightly more parsimonious (difference in AIC values for the two models = 0.84) than one that provided separate estimates. Estimated nesting success was 0.33 for American Robins when cover type was ignored (Table 2); when estimated separately, success was 0.29 in aspen and 0.35 in cottonwood.

Table 2. Average reproductive success and population growth rate (λ) for American Robin and Yellow Warbler in two cover types as derived from field measurement or computer simulation.

Species (no. of nests)	No. of stands	Elevation class (m)	Cover type	Measured nest success	Range of nest initiation dates (SE)	Cowbird parasitism, % (SE)	Deterministic estimate of λ
American Robin (441)	5	1000–1500	cottonwood	0.33	72.8 (3.8)	0.0	1.17
	4	2000–2500	aspen	0.33	58.8 (2.3)	0.0	1.00
Yellow Warbler (340)	5	1000–1500	cottonwood	0.22	41.2 (3.9)	44.2 (3.3)	0.94
	4	2000–2500	aspen	0.40	18.5 (0.9)	8.7 (4.2)	0.89

In contrast, Yellow Warbler nesting success was much lower in the cover type with more-intense land use. For this species, a model that provided separate estimates of daily survival rate for aspen and cottonwood stands was much more parsimonious (difference in AIC values for the two models = 4.4) than one that provided a single estimate. Estimated nesting success was 0.40 in aspen but only 0.22 in cottonwood (Table 2). A model that replaced cover type with home density within 6 km of a stand was slightly more parsimonious (difference in AIC values = 0.6) and indicated that land-use intensity was negatively related to nesting success (regression coefficient for home effect = -0.003 [95% CI: -0.001 to -0.005]).

For nests that were successful, production of young did not differ ($p > 0.21$) by cover type in either species. For the American Robin, successful nests fledged 3.0 young (SE = 0.1, $n = 60$) in aspen and 2.8 young (SE = 0.1, $n = 161$) in cottonwood. Successful Yellow Warbler nests fledged 2.9 young in aspen (SE = 0.2, $n = 29$) and 2.8 young in cottonwood (SE = 0.1, $n = 98$).

Interactive Effects of Biophysical Factors and Land Use on Net Population Growth

Estimated female success for American Robins was 0.54 in aspen and 0.76 in cottonwood stands when nesting success (0.33 in each cover type) and potential re-nesting opportunity were combined. Given that the two cover types yielded similar estimates of females fledged per successful female and were assigned the same juvenile and adult survival rates, λ was estimated as higher in cottonwood (1.17) than in aspen (1.00) (Table 2). Thus, for American Robins, our data and modeling indicate that low-elevation hotspots with lengthier breeding seasons may act as important population source areas.

In contrast, results for the Yellow Warbler indicated that both cover types may potentially be population sinks. The longer nesting season in cottonwood caused our estimate of female success (0.53) to be well above estimated nesting success (0.22) in this habitat. Nesting success in cottonwood was so low, however, that even when repeated re-nesting increased female success, our model still estimated that the habitat was a population sink ($\lambda = 0.94$). In aspen, the short nesting season prevented female success (0.41) from being substantially higher than nesting success (0.40). Consequently, aspen was also estimated to be a population sink ($\lambda = 0.89$).

Simulations of net population growth for Yellow Warblers under current home densities revealed that the study area was a strong population sink, with population growth negative both in nature reserves because of elevation constraints and on private lands because of land-use constraints (Table 3). Net population growth of Yellow Warblers was positive only on public lands at mid-elevations where elevation constraints were intermediate and home densities are low. When the home effect was removed from the model, the study area was projected to be a strong population source area, with negative population growth only in nature reserves.

Discussion

Our results indicate that bird species richness and abundance were high only in the small portion of the landscape where biophysical factors were favorable. Because nature reserves in our study area occurred at higher elevations, avian hotspots were found primarily outside reserves, with the majority located on or near private lands. Biophysical factors constrained reproduc-

Table 3. Simulated population dynamics of Yellow Warblers in the study area with and without the influence of rural residences.

Ownership	Area (ha)	Current population size	Simulated net annual population change without home effect	Simulated net annual population change under current home densities
Private	808	2942	309	-85
Public, general	4251	2003	41	6
Public, nature reserves	984	804	-28	-35
Total			322	-114

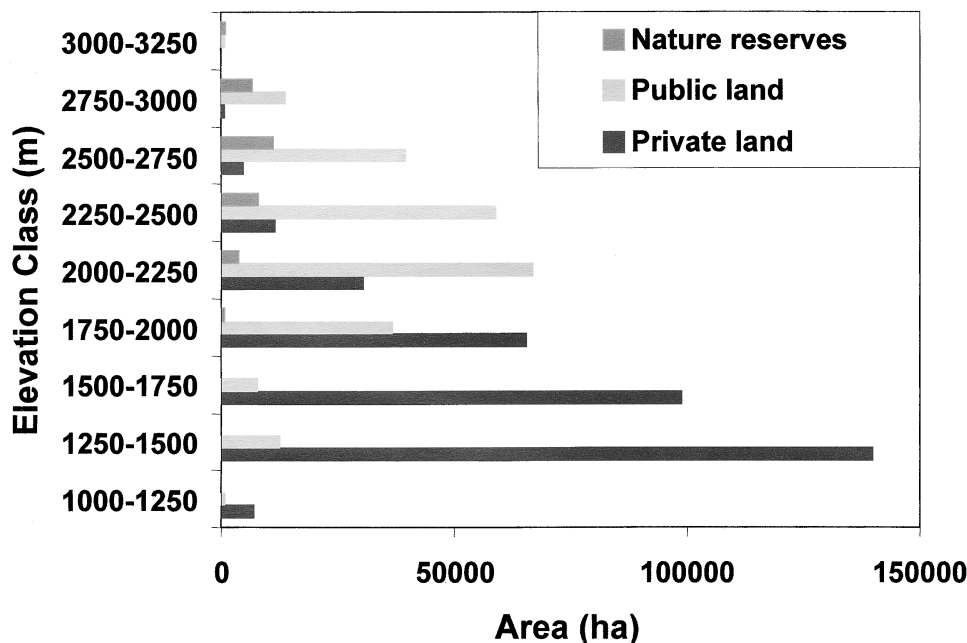


Figure 3. Elevational distributions of nature reserves (U.S. national parks and national wildlife refuges, U.S. wilderness areas), other public lands, and private lands across the study area.

tion in the American Robin and Yellow Warblers. Climate conditions at higher elevations resulted in short breeding seasons and little opportunity for renesting. Consequently, the estimated λ for both species was lower in aspen (intermediate elevation) than in cottonwoods (low elevation). For the American Robin, estimated λ in aspen was near 1.0, the threshold where net population growth is 0. In cottonwoods, estimated λ was well above 1.0, suggesting that this habitat is a population source for this species. We speculate that deciduous habitats at high elevations in the study area were population sinks because of the short breeding season.

Land use also influenced bird reproduction. Within private lands, rural residential development was located disproportionately close to bird hotspots. High densities of homes and associated high rates of nest predation and parasitism in cottonwoods likely depressed reproduction of Yellow Warblers below that expected based on the favorable elevation of these sites. Thus, our estimated λ for the Yellow Warbler was well below replacement levels both in cottonwood stands with high land use and in aspen stands at high elevations where the nesting season was shorter. A simulation that removed the effect of home density suggested that low-elevation hotspot habitats were strong population sources prior to rural residential development, whereas high-elevation habitats were population sinks because of the short breeding season. These results are consistent with the possibility that for some bird species population sources can be converted to population sinks by intense human use.

In total, our results suggest that the location of nature reserves in less favorable landscape settings and the concentration of intense land use in more favorable landscape settings have important implications for maintaining biodiversity. The population sizes of species in nature reserves at high elevations may be substantially constrained by unfavorable climate, infertile soils, aridity, and/or low food availability. If net population growth is sufficiently low in such reserves, small population sizes and increased likelihood of extinction are expected. Such populations within reserves may be bolstered by immigrants from population source areas in more-favorable landscape settings outside reserves. If intense land use converts such population sources to sinks, increased risk of species' extinction within nature reserves may result.

Our ability to rigorously estimate population growth was impaired, however, by lack of data for some vital rates. In particular, monitoring nesting histories of individually marked birds would allow estimation of renesting potential and the frequency of multiple broods and would permit researchers to evaluate the importance of these factors to reproductive output. Given the assumptions we made in modeling, we can envision reasons that our estimates of λ might be too high or too low. Our model, which allowed up to three renesting attempts, may have allowed for more renesting by American Robins and Yellow Warblers than is realistic and thus may have biased estimates toward high value of λ . But this was unlikely a large source of bias because renesting is well documented in both species, and initial

renewing attempts were most important to our results. Furthermore, other studies have shown that birds adjust to environmental variation by adjusting the number of renewing attempts (Rodenhouse & Holmes 1992). In contrast, our estimates of λ for American Robin may be biased toward low values because we did not allow double brooding, which probably does occur to some extent in this species at northern latitudes and would increase estimates of λ .

Future estimates of the interactive effects of biophysical factors and land use on net population growth would be improved if data were obtained in multiple years across a range of climate and land-use conditions while controlling for cover type. Such a design would be less confounded than ours and would provide estimates of spatial and temporal variation in vital rates. Such a design will be extremely difficult to implement, however, given the spatial patterning of climate, cover types, land ownership, and land use. Furthermore, field estimates of survival rates of juveniles and adults will likely remain elusive for passerines, especially across a range of covariate conditions. Despite these difficulties, we do believe that future research designed to improve our understanding of the spatial patterning of demographics is warranted given the rapid changes occurring on private lands found in favorable biophysical settings.

Further study is needed to determine how interactions among biophysical factors, land use, and source-sink population dynamics may influence other groups of species in the Greater Yellowstone Ecosystem. We speculate that such interactions may explain the extinction of arctic grayling (*Thymallus arcticus*), the near extinction of the Trumpeter Swan (*Cygnus buccinator*), and the current precipitous drop in pronghorn antelope (*Antilocapra americana*) in Yellowstone National Park (Hansen & Rotella 2002). We further speculate that these factors influence species in other nature reserves where harsh biophysical factors constrain distributions of native species and human land use.

Assessment of the biodiversity consequences of the nonrandom location of many of the world's nature reserves is especially important now. Our findings suggest that alteration and destruction of the remaining productive habitats outside nature reserves will pose dire threats to many wildlife populations. Globally, human population density and growth rates are disproportionately high near biodiversity hotspots (Cinotta et al. 2000). Both human population density and land-use intensity are now increasing on the private lands surrounding nature reserves (Newmark 1996). Thus, seminatural habitats outside nature reserves are likely declining, possibly reducing the size of population source areas. These trends cast doubt on the viability of current strategies that rely on nature reserves for wildlife conservation and ignore intervening lands. Conservation strategies to protect population source areas outside reserves

are likely necessary to reduce rates of future extinction in nature reserves.

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