

Ecological Causes and Consequences of Demographic Change in the New West

ANDREW J. HANSEN, RAY RASKER, BRUCE MAXWELL, JAY J. ROTELLA, JERRY D. JOHNSON, ANDREA WRIGHT PARMENTER, UTE LANGNER, WARREN B. COHEN, RICK L. LAWRENCE, AND MATTHEW P. V. KRASKA

Rural areas in the American West are undergoing a dramatic transition in demography, economics, and ecosystems. Long known as the “Wild” West, the region has been characterized by low human population densities and vast tracts of unsettled or undeveloped land (Wilkinson 1993, Power 1998). For most of the 1900s, the population of many rural areas in the West grew very slowly or even decreased. Because local economies were based on natural resource industries such as mining, logging, farming, and ranching, many residents of the region considered conservation strategies on public lands detrimental to local economic development. Efforts to establish nature reserves and to preserve public lands from commercial development were seen as restricting the use of vital natural resources.

In recent decades, parts of that Wild West have given way to the “New” West (Riebsame et al. 1997). People from throughout the United States have been migrating to the Rocky Mountains and the inland West. With a population growth rate of 25.4%, the mountain West was the fastest-growing region of the country during the 1990s. Surprisingly, rapid population increases are occurring not only in urban areas such as Denver and Salt Lake City but also in rural counties, many of which are gaining population even faster than urban areas (Theobald 2000). Some 67% of the counties in the Rocky Mountains grew faster than the national average during the 1990s (Beyers and Nelson 2000). Consequently, small cities such as Bozeman, Montana, and Moab, Utah, are beginning to experience traffic congestion and sprawl.

Some of the rural population growth in the New West represents an intraregional redistribution of people from the high plains, which continue to lose population (Johnson 1998), to more mountainous areas. Many of the new residents, however, are in-migrants from other regions throughout the United States (Riebsame et al. 1997). The residents of a rural

AS NATURAL AMENITIES ATTRACT PEOPLE AND COMMERCE TO THE RURAL WEST, THE RESULTING LAND-USE CHANGES THREATEN BIODIVERSITY, EVEN IN PROTECTED AREAS, AND CHALLENGE EFFORTS TO SUSTAIN LOCAL COMMUNITIES AND ECOSYSTEMS

subdivision in a boom county in Montana might include recent arrivals from big East Coast cities, midwestern farms, and the nearest small town. Among the in-migrants are retirees, wealthy young adults, and professionals in computer technology, real estate, and other service industries (Nelson 1999).

Several of the authors work at Montana State University, in Bozeman: Andrew J. Hansen (hansen@montana.edu) and Jay J. Rotella are associate professors, and Ute Langner is a research associate, in the Ecology Department; Bruce Maxwell is an associate professor in the Land Resources and Environmental Science Department, and Rick L. Lawrence is an assistant professor of remote sensing with the Mountain Research Center in that department; and Jerry D. Johnson is an associate professor in the Political Science Department. Matthew P. V. Kraska is development coordinator for the Big Sky Institute, Montana State University. Ray Rasker is the director of the Northwest Office of the Sonoran Institute in Bozeman, MT 59715. Andrea Wright Parmenter is a research associate at the Center for the Environment, Cornell University, Ithaca, NY 14853. Warren B. Cohen is a research forester with the US Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331. © 2002 American Institute of Biological Sciences.

In association with the population expansion, many professional, service, and high-technology businesses are relocating to the region.

It is not yet fully clear why the rate of population growth, economic conditions, and land-use patterns change more rapidly in some areas of the West than in others. Some counties are growing quickly while others in the same region are losing population. Residents are confused about how fast and how much the balance between traditional resource-based industries and the newer high-technology and recreation industries will change. Also, the effects of population growth on land cover and land use are poorly quantified. The rates at which urban and rural residential areas are expanding while agricultural lands and natural habitats are contracting have not been widely analyzed.

There is also uncertainty about why people and businesses are attracted to the mountain West. While improved electronic connectivity and transportation make living and working in rural areas easier (Levitt 2002), considerable impediments remain, including slow or limited Internet access, long distances to markets, the absence of a trained work force, and harsh climate. One view is that the region is attractive despite these impediments because of its "natural amenities," including scenery, wilderness, outdoor recreation, and wildlife (Johnson and Rasker 1995, Beale and Johnson 1998). Many newcomers speak of the "one-hour rule": They want to work within an hour's drive of good fishing, hunting, skiing, and hiking. Taking exception to the traditional view that the environment and the economy are in conflict, many economists in the New West argue that a high-quality environment is the region's greatest economic asset (Rasker 1993, Power 1998).

Another issue is the influence of human development on ecosystems. There is a general sense in the region that the emerging economy, based on high technology and outdoor recreation, is more consistent with conservation than is the traditional extraction-based economy. Initial studies suggest, however, that the growing population is altering ecosystem processes and biodiversity because of where people are choosing to live and play (Theobald 2000). Increasingly, long-time and new residents alike are opting to live "out of town" in rural areas. Hence, sprawling subdivisions and ranchettes are replacing natural habitats and agricultural lands. At the same time, rates of recreational activity along rivers, in forests, and on backcountry trails are soaring (Laitos and Carr 1999), with native wildlife being displaced as a result (Miller et al. 1998). Besides affecting private lands, development near the boundaries of national parks and other protected parcels may have an impact on those areas as well. Effects on protected areas may include the loss of native species, changes in disturbance regimes (such as wildfire), and the spread of invasive organisms.

An overview of the present study

In this study, we focus on the Greater Yellowstone Ecosystem (GYE) in examining the ecological causes and consequences of demographic change in the New West. In summarizing

research that we have conducted in the area since 1993, we address three questions:

- How fast are humans expanding into seminatural landscapes in the rural West?
- To what extent is this in-migration related to ecosystem qualities rather than socioeconomic factors?
- How is human development in rural areas of the West influencing biodiversity in and around nature reserves?

We first describe GYE and quantify socioeconomic and ecological change during the period 1975–1995. We then examine possible socioeconomic and ecological drivers of population growth. The impact of rural residential development on wildlife is then considered, especially its effects in nature reserves. We end by considering implications for research and management in GYE and other western landscapes. Answers to the questions we raise in the present article are important because they may enable growth strategies designed to minimize negative ecological impacts on private and public lands. Beyond their value for conservation, strategies to protect scenery, water quality, wildlife, and the sense of wilderness may also be key to sustaining economic growth in the New West (Rudzitis 1999).

The Greater Yellowstone Ecosystem

GYE was originally defined as the range of *Ursus arctos*, the Yellowstone grizzly bear (Craighead 1991). For this study and its broader goals, however, we define GYE as the contiguous area of public lands and surrounding private lands down to and including the high plains that surround the mountainous ecosystem (Figure 1). For the socioeconomic analyses, we considered an expanded area that includes the 20 counties of GYE because socioeconomic data generally are not available at jurisdictional levels finer than the county. GYE's public lands include two national parks (Yellowstone and Grand Teton), seven national forests, and more than 20 other federal and state jurisdictions (Goldstein 1992). Yellowstone National Park (YNP) is among the best-known nature reserves in the world. The park and surrounding public lands represent a vast area of wild and seminatural habitats. These lands are unique in the lower 48 states in supporting several large carnivores, such as the grizzly bear and free-roaming populations of large ungulates (Schullery 1997). In the privately owned lowland valleys, land use is most likely to be devoted to agriculture, grazing of domestic animals on rangeland, rural housing, and urban development. The 20 counties of GYE had 359,492 residents in 2000, most living in and around small cities and towns.

The region has strong gradients in topography, climate, and soils. The national parks of GYE are relatively high in elevation and center on the Yellowstone Plateau and surrounding mountain ranges. Other public lands are largely at middle elevations on the flanks of the plateau. In striking contrast, private lands are primarily at lower elevations in valley bot-

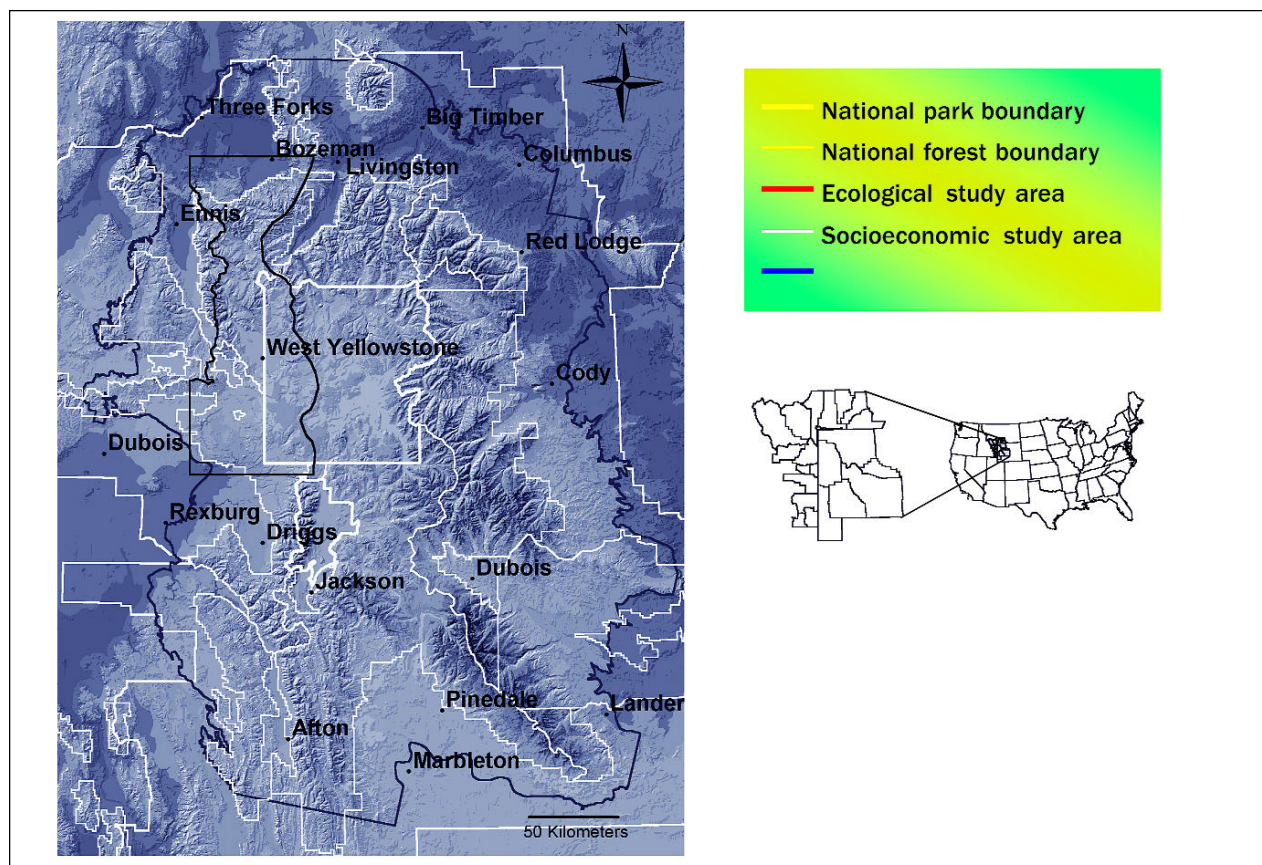


Figure 1. A relief map of the Greater Yellowstone Ecosystem (GYE). We conducted ecological analyses for the watersheds of GYE down to and including the high plains that surround the ecosystem. The lower elevational boundary varied from 1280 to 1800 meters. For the socioeconomic analyses, we considered an expanded area that included the 20 counties of GYE because socioeconomic data generally are not available at jurisdictional levels below that of the county.

toms and on the plains surrounding the public lands. 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 alluvial soils that are higher in nutrients and water-holding capacity. Climate severity increases with elevation. The length of the growing season varies from 5 to 6 months in the valley bottoms to about 2 months in subalpine forests (Despain 1990). Much of the precipitation falls as snow. The average snowmelt date varies from about May 1 at lower elevations to July 1 in high-elevation forests.

The vegetation of GYE is a mosaic of forests, shrublands, and grasslands. Coniferous forests drape much of the Yellowstone Plateau and mountain slopes. Arid shrublands and grasslands exist on fine-textured soils from valley bottoms up to mid-slopes and in the alpine zone. Aspen (*Populus tremuloides*) is distributed in relatively small patches, primarily on moist toeslopes or on fractured rocks. Riparian zones in larger floodplains are dominated by cottonwood (*Populus spp.*) and willow (*Salix spp.*). Unfavorable climate and soils cause primary productivity rates to be low over much of

GYE and relatively high only in valley bottoms (Hansen et al. 2000). Both fire and logging are common disturbances in GYE. Approximately 45% of YNP burned during 1988 (Romme and Despain 1989). Logging was common on most of the national forests from 1960 to 1990, but little logging has occurred in recent years.

Like many areas in the inland West, GYE is changing. Movie stars, corporate executives, and many others are relocating there. The local economy is shifting from traditional resource industries to a New West economy based on a mix of the traditional with new sectors such as high technology, real estate, and recreation. Local communities are confronting traffic congestion and rural sprawl as major issues. However, rates of change are poorly quantified, interactions between economy and ecology are hotly debated, and strategies for conserving wildlife across public and private land boundaries are poorly developed.

Change in GYE: 1970–1997

To determine how rapidly socioeconomic and ecological conditions have changed in GYE in recent decades and how the patterns of change vary across its 20 counties, we compiled

data from the US Bureau of the Census, the Bureau of Economic Analysis of the US Department of Commerce, county assessors' offices, satellite imagery, and other sources for the period 1970–1997. Using these data, we compiled averages for GYE, as well as averages for the GYE counties grouped into three classes of population change over the period 1970–1997: slow (–6% to 14%, 5 counties); intermediate (27% to 58%, 10 counties), and fast (68% to 185%, 5 counties).

Population size. The population of GYE increased 55% between 1970 and 1997, a growth rate exceeding that of three-quarters (78.2%) of all counties in the United States (Figure 2). This overall figure masks the wide variation among GYE counties. The population of the five fastest-growing counties in GYE increased 107.2% overall; these counties are in the top 10th percentile of counties in the United States in growth rate. Among this group was Teton County, Wyoming, which contains the Grand Teton National Park gateway community of Jackson, the adjacent Teton County, Idaho, which is a bedroom community for Jackson, and Gallatin County, Montana, which includes Montana State University and the high-technology center of Bozeman. In contrast, five GYE counties grew slowly, at an average overall rate less than 15% over the 27-year period. These counties lie largely on the high plains on the periphery of GYE. Relatively

distant from the national parks, these counties had economies that were dominated by agriculture or mining.

Economics. The economy of GYE, like that of much of the West, was growing and diversifying away from a reliance on resource extraction and agriculture (Power 1991, Rasker 1991). Mining, oil, gas, timber, farming, and ranching collectively accounted for 19% of total personal income in the region in 1970; by 1995 they accounted for 6%. Over 99% of the net growth in personal income from 1970 to 1995, in real terms, was in industries other than the historical staples of the region. These growth sectors included business, engineering, health care, and other services, which accounted for 26% of net new income growth; and nonlabor income sources, which accounted for another 51% of growth. The economy of the region broadened to include employment in a variety of business and producer services, such as finance, insurance, real estate, telecommunications, software development, research, and management consulting. Many of these were “footloose,” in the sense that the owners of such businesses often were not tied to a particular location and therefore could relocate to desirable areas (Rasker and Glick 1994).

While GYE on average was growing and diversifying, there were differences among counties. The five fast-growing counties conformed to the GYE-wide trend of rapid growth in personal income in nontraditional sectors during 1970–1997 (Figure 3). These counties were characterized by a lack of historical reliance on mining, rapid growth of both professional and service industries, high growth in relatively high-paying services, and relatively modest growth in nonlabor income sources (primarily money earned from past investments and retirement income, or income related to the presence of relatively elderly residents, including Medicare payments). Among these five fastest-growing jurisdictions, Stillwater County, Montana, was an anomaly because of relatively stable mining employment secured by a successful platinum and palladium mine, one of the few in the world. Even so, across the five counties, personal income earned in mining represented only 2% of net new income growth.

In contrast, personal income increased much more slowly in the five slowest-growing counties (Figure 4). These counties were more heavily dominated by agriculture and mining in 1970. Both of these

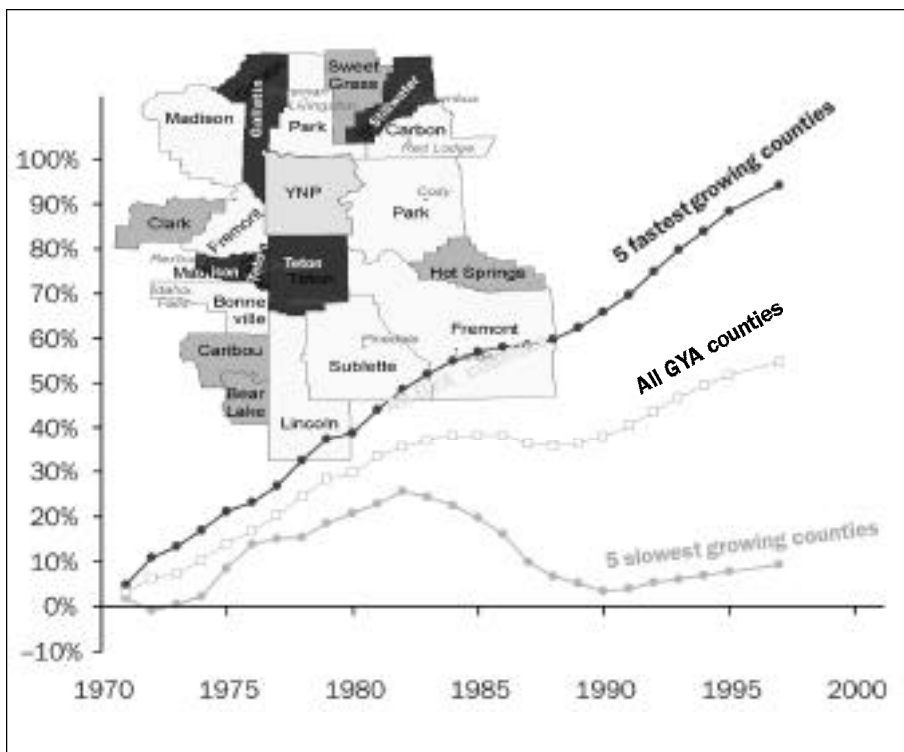


Figure 2. Human population change in the Greater Yellowstone Ecosystem, 1970–1997. Shown are the overall rate of human population growth in the 20 GYE counties, in the 5 fastest-growing counties, and in the 5 slowest-growing counties, during the period 1970–1997.

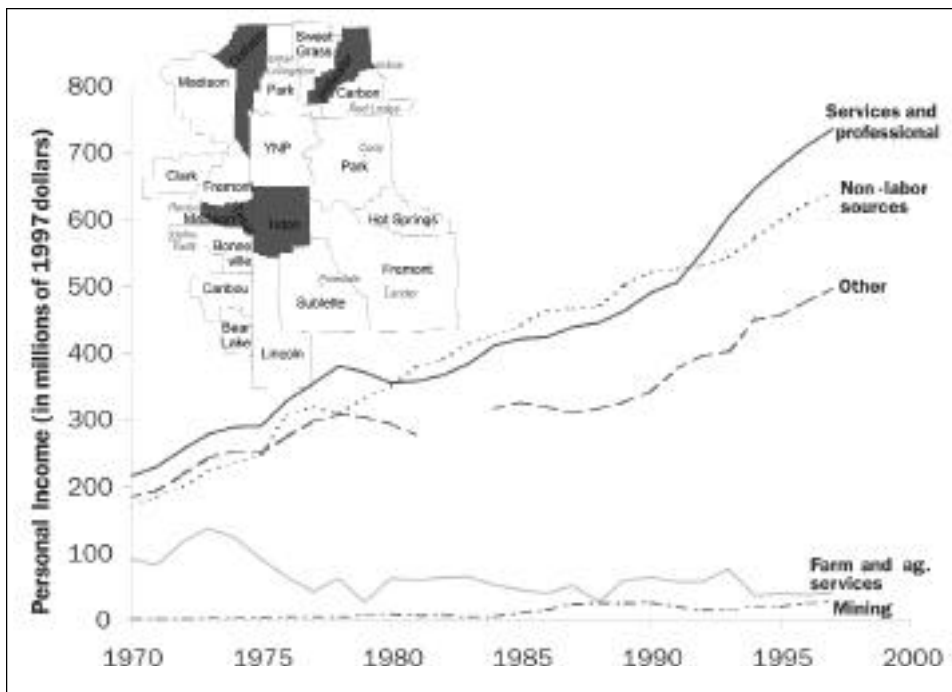


Figure 3. Rate of growth in personal income derived from major economic sectors for the five GYE counties whose human populations were growing the fastest. Gaps in the trend lines indicate missing data.

sectors saw decreases in total personal income from 1970 to 1997. Growth in service and professional occupations was relatively slow during this period. As a consequence, the most significant contributor of new income since 1970, in real terms, was nonlabor sources, which accounted for 97% of net new personal income. Thus, most counties traditionally dependent upon agriculture and mining experienced relatively slow growth in population size and personal income, with the bulk of this in retirement and investment income. In contrast, some other counties in GYE experienced rapid increases in population and personal income in the service and professional sectors as well as in the nonlabor sector. These trends lead to the question of why some GYE counties are booming while others are relatively stagnant.

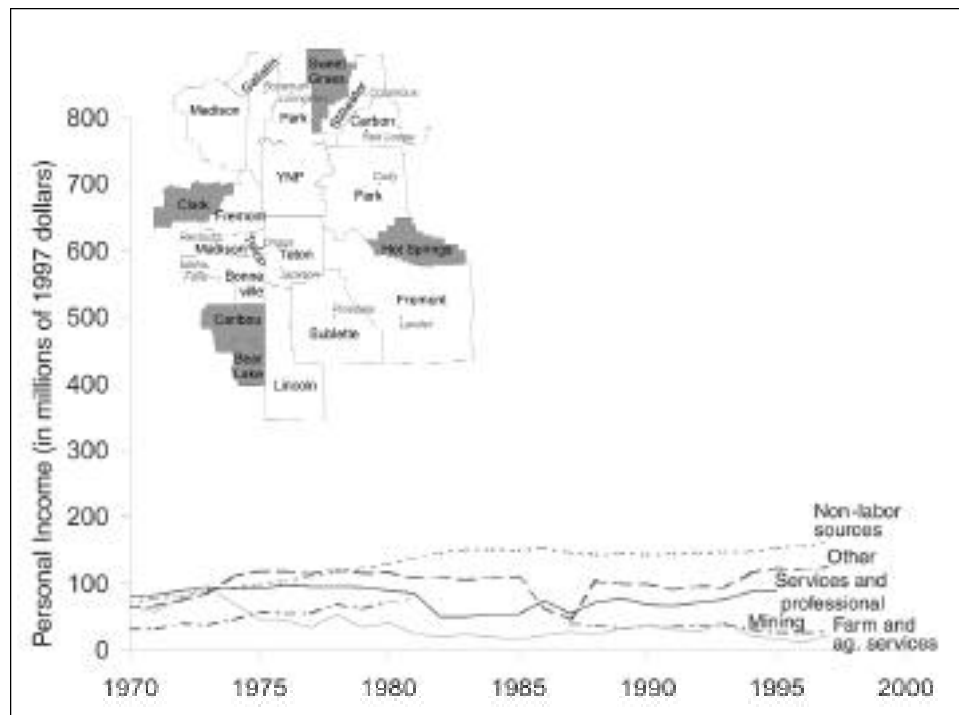


Figure 4. Rates of growth in personal income derived from major economic sectors for the five GYE counties whose human populations were growing the slowest. Gaps in the trend lines indicate missing data.

Land cover and land use. Associated with demographic and economic expansion were changes in land cover and land use. We recently completed the first fine-resolution maps of land cover for the entire GYE. These maps were derived from Landsat satellite imagery for 1975, 1985, and 1995. Here we summarize changes in land cover for the period 1975–1995.

Across GYE, the area of the dominant cover types, conifer and mixed conifer (conifer and herbaceous), decreased by 2% from 1975 to 1995 (Figure 5). This small reduction masked wide changes in the distribution of forest cover and seral stages. The area in conifer (greater than or equal to 70% conifer cover) decreased by 17%, while areas of mixed conifer (10%–70% conifer cover)

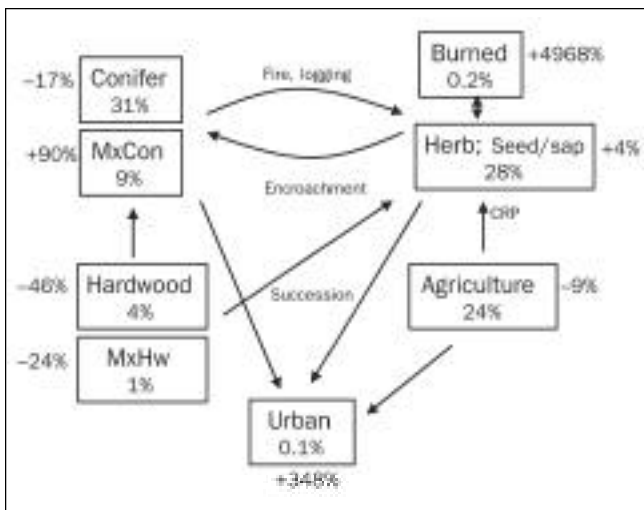


Figure 5. Change in land cover and land use in the Greater Yellowstone Ecosystem during 1975–1995. Data within the boxes are the proportions of total study area for each cover type in 1975. Data outside the boxes are the percentage changes in each cover type during 1975–1995. Cover types are agriculture (cropping and intensive grazing), burned (by wildfire or prescribed fire), conifer (more than 70% conifer cover), hardwood (more than 70% hardwood cover), herbaceous (natural grassland), seedling/sapling (recently disturbed conifer stands), mixed conifer (less than 70% conifer cover), mixed hardwood (less than 70% hardwood cover), and urban.

increased by 90%. Some areas in conifer in 1975 were subsequently logged, or burned in the 1988 wildfires, and became either burned, herbaceous, or mixed conifer by 1995. Some of the gain in mixed conifer was also due to the encroachment of conifers into nonconifer habitats because of fire exclusion or climate change. Consequently, areas of hardwood (greater than or equal to 70% hardwood) decreased by 46%, and mixed hardwood cover (10%–70% hardwood) by 24%, from 1975 to 1995. The area in agriculture decreased by 9%, partially because of conversion to grassland under the Conservation Reserve Program, a federal program that pays farmers to leave marginal croplands fallow. The proportion of land occupied by urban areas increased substantially (348%), largely at the expense of agriculture. Urban expansion occurred mostly at the edges of cities and towns, although entirely new communities, such as the ski resort town of Big Sky, Montana, had been developed since 1970 (Oechsli 2000).

We classified homes outside urban boundaries as rural residential development (RRD). The locations of these rural homes were inferred from county assessor and water-well permit records. These data were available for the Montana and Wyoming portions of GYE. During 1970–1997, RRD increased more than 400% in this portion of GYE. Expansion of RRD was pronounced around population centers. RRD also increased in relatively remote parts of GYE, particularly along

the major river valleys coming off the Yellowstone Plateau and the surrounding mountains (Figure 6).

The counties with the highest population growth rates had the largest increases in urban and RRD lands during 1975–1997. The extent of urban area increased 377% in the fast-growth counties, compared with 147% in the slow-growth counties. Similarly, RRD increased by 167% and 36%, respectively, in fast-growth and slow-growth counties.

Socioeconomic causes and consequences of change

We suggested in the introductory paragraphs of this article that many of the new people and businesses in the West have been attracted by natural amenities. The contributions of such ecosystem-based factors, relative to traditional socioeconomic factors, however, are little known.

The term *natural amenities* has not received a standard definition from sociologists. The Economic Research Service of the US Department of Agriculture has devised a “natural amenities index” based on three classes of physical factors: climate, topography, and water area (Cromartie and Wardell 1999). Such factors were selected as representing the base ingredients of natural amenities such as scenery and outdoor recreation. Population growth in rural counties in the United States was strongly correlated with this natural amenities index during 1970–1996 (McGranahan 1999). Surveys of new residents and businesses in counties with high levels of natural amenities found that factors such as scenery, environmental quality, pace of life, outdoor recreation, and climate were more important reasons for relocation than job opportunity or cost of living (Johnson and Rasker 1995, Rudzitis 1999). Rapid population growth was also associated with proximity to wilderness, and residents frequently cited access to wilderness as important to them (Rudzitis and Johansen 1991). Wildlife presence might influence economic development by supporting hunting, fishing, wildlife viewing, and sense of wilderness (Ingram and Lewandrowski 1999). In sum, these studies suggest that emigrants to the New West are seeking mountainous or coastal scenery; access to outdoor recreation, including hiking, fishing, hunting, and skiing; proximity to open space and wilderness; and moderate climate. For the present study, we refer to scenery, outdoor recreation, wildlife, sense of wilderness, and the biophysical factors that contribute to these as natural amenities.

We tested the extent to which biophysical factors were correlated with rates of population growth in rural counties of Idaho, Montana, and Wyoming (Rasker and Hansen 2000). The factors we considered involved climate, topography, water area, forest area, and area in nature reserves. We found that population growth was significantly associated with mountainous topography, forest cover, greater precipitation, and the presence of nature reserves. These results were consistent with the hypothesis that natural amenities contribute to population growth across the three states.

Within GYE, we examined the importance of biophysical factors relative to socioeconomic variables as explanations for

population growth (Rasker and Hansen 2000). As was true in the three-state analysis, biophysical factors explained a significant proportion of the variability in population growth among counties, sometimes as much as 60%. Some socioeconomic factors, however, were also significant. These included education level of the work force, percentage of employment in business services, and the presence of an airport with daily commercial service to larger markets. Ecological and socioeconomic variables together explained 79% of the variation in population growth. These results suggested that any model for economic development should explicitly acknowledge the role that natural amenities play in population growth. Although natural amenities may be a necessary condition for the growth of rural counties in GYE, however, they are probably not sufficient. Socioeconomic factors involving education, labor, and transportation are also likely to be important.

Consequences for biodiversity

One measure of how the changes in land cover we have noted are influencing ecosystem properties is the biodiversity of native species. It is widely assumed that increases in urbanization and RRD have a limited influence on wildlife in the public lands of GYE because these developments are confined to private lands, which represent only 36.4% of the land area. Further, the level of human density on these private lands is very low relative to that in much of the United States. Our results suggest, however, that increasingly intense land use has affected many native species in and around the public lands in GYE, largely because of where people live on the landscape.

We focused our detailed analyses on bird species because many species of diverse taxa and life-history types could be sampled within logistic constraints (Hansen et al. 1999, 2000, Rotella et al. 2000, Hansen and Rotella 2002). We first quantified the distributions of native bird species and of bird species richness across the landscape relative to habitat type, elevation, and ownership. We then measured reproductive output of selected species across gradients in natural factors and land-use intensity. We used our empirical data and models of population dynamics to estimate the effects of RRD on two bird species across the study area and within YNP. Finally, based on the results of the bird analyses, we speculated on how other vertebrates may have been affected by land use in GYE.

Bird distribution. The analysis was restricted to a 9500-square-kilometer area in the northwest portion of GYE that included the upper Gallatin, Madison, and Henry's Fork watersheds (Figure 1). Species abundances were sampled during 1995–1997 at 100 sites, which were stratified by cover type,

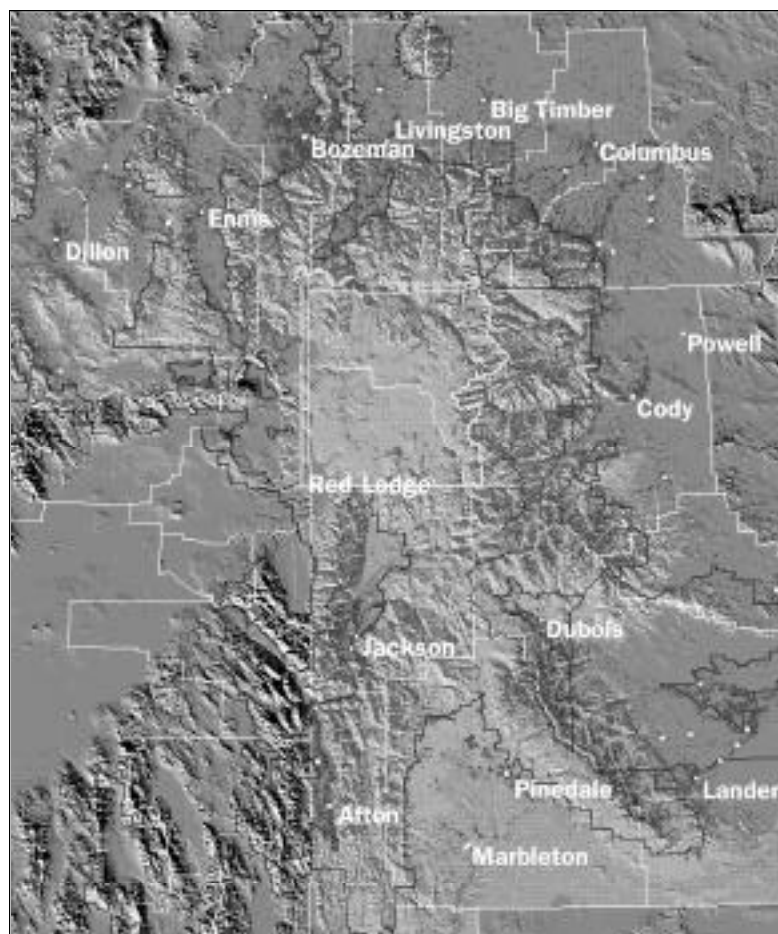


Figure 6. Distribution of rural homes in the Montana and Wyoming portions of the Greater Yellowstone Ecosystem. Each white dot indicates a home site, based on county well records. Blue lines indicate the boundaries of public lands; the yellow polygon is Yellowstone National Park.

seral stage, and elevation class (Hansen and Rotella 2002). Several biophysical factors were quantified at the sites, including elevation, slope, aspect, specific catchment area, parent material, aboveground net primary productivity, and vegetation structural complexity. A type of multiple regression analysis termed *mixed modeling* (SAS Institute 1996) was used to quantify relationships between bird species richness and total bird abundance and the biophysical predictor variables. The best models were then used to extrapolate bird species richness and total bird abundance over the study area, and these data were analyzed by elevation and land ownership.

We found that bird species richness, total bird abundance, and individual bird species abundances were strongly associated with landscape settings with one or more of three features: lower elevation, the presence of alluvial parent materials, and higher aboveground net primary productivity. Hardwood forests (aspen, cottonwood, and willow) dominated these sites. Extrapolating species richness and total bird abundance across the study area revealed that bird “hot spots” were

relatively rare (Figure 7). We defined hot spots as places predicted to have at least 60% of maximum richness and bird abundance, a threshold consistent with those applied in other hot-spot mapping efforts (e.g., Brooks et al. 2001). These hot spots covered only 2.7% of the study area and were primarily at lower elevations. Several individual bird species were largely restricted to these hot spots. Among the 71 species analyzed, 23% were found only in the three hardwood habitats, and 49% were significantly associated with these habitats.

Bird habitats were not randomly situated relative to land allocation and land use. Private lands and intense land use were biased toward the productive, low-elevation settings that were especially important for native species. Among the areas in bird hot spots, 67% were on or within 6 km of private lands, while only 6.5% were in nature reserves. Within private lands, RRD was placed disproportionately close to bird hot spots. For example, home densities within 2 km of hot spots were 67% higher than they were at random locations on private lands.

Bird species that either prey upon other birds or are brood parasites were more abundant near RRD. Avian nest predators such as the black-billed magpie (*Pica pica*) and the common raven (*Corvus corax*) were significantly associated with density of homes within 6 km of bird hot spots. This was also true for a brood parasite, the brown-headed cowbird (*Molothrus ater*). These species are attracted to home sites by food associated with hobby livestock, compost piles, garbage, and pet feeding (Marzluff et al. 2001). From locations near rural homes, these birds venture into areas of natural vegetation such as hardwood forests and prey upon or parasitize the nests of other bird species.

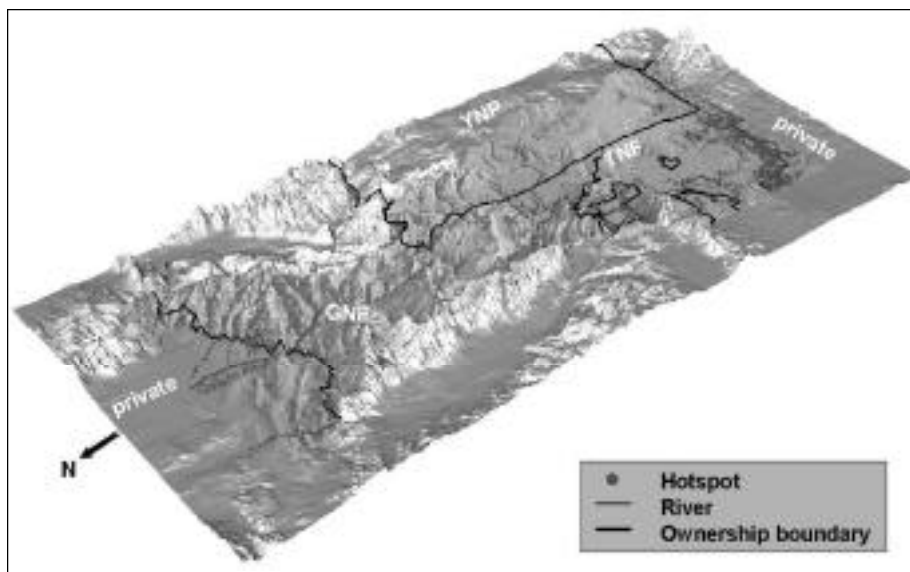


Figure 7. Distribution of bird hot spots (areas of bird species richness and total abundance greater than or equal to 60% of maximum) across the bird study area. YNP, Yellowstone National Park; TNE, Targhee National Forest; GNF, Gallatin National Forest. From Hansen and Rotella (2002).

Bird population dynamics. We also evaluated the relative effects of biophysical factors and land use on bird reproduction by monitoring nests of two bird species, the American robin (*Turdus migratorius*) and the yellow warbler (*Dendroica peckia*), in two hot-spot habitats—cottonwood and aspen—that differed in elevation and land use (Hansen and Rotella 2002). These species were selected because large samples of nests could be obtained and because these species differ in susceptibility to nest predation and parasitism by cowbirds. American robins aggressively defend their nests against brood parasitism and predation. Yellow warbler nests are commonly parasitized by cowbirds. We estimated nest success using the methods of Rotella and others (2000) and estimated population growth rate (λ) based on simulated female success, females fledged per successful nest, and published estimates of adult and juvenile survival. Female success was estimated with a stochastic model that incorporated field estimates of nest success, average age of failed nests, and the duration of the nest initiation period by elevation class.

Reproduction of American robins was greater at lower elevations. The longer breeding season in low-elevation stands allowed more time for renealing. Moreover, we found no parasitism of robin nests by cowbirds. The estimated population growth rate for American robins was well above the replacement level of 1.0 in low-elevation stands and close to 1.0 in the high-elevation stands. This suggests that low-elevation habitats might be population source areas for this species and that reproduction rates were lower in high-elevation stands, where the length of the breeding season was shorter.

The population growth rate for the yellow warbler was well below the replacement level of 1.0 at high-elevation sites, most likely because the short breeding season precluded renealing.

At lower elevations, despite the longer breeding season, the estimated population growth rate for yellow warblers was also below the replacement level in the low-elevation cottonwood stands. This was probably because of the effects of land use at low elevations and elevated nest predator and cowbird populations. Yellow warbler nest success was negatively related to density of homes within 6 km. Moreover, density of homes within 6 km was higher around cottonwood stands than around aspen stands. The densities of both cowbirds and avian nest predators were positively related to home density and were higher in cottonwood than in aspen stands. Yellow warblers incurred high rates of parasitism in cottonwood (44.2% of nests) and very low nest success

(22%). These results suggest that the entire study area was a population sink for yellow warblers because of climatic constraints at higher elevations and land-use constraints at lower elevations.

To better understand the influence of land use on the population dynamics of the yellow warbler, we used a computer model to simulate net population growth across the study area as a function of bird abundance, elevation, and density of rural homes within 6 km. Current home density was used in one analysis, and a second analysis simulated a presettlement condition by removing the home density effect. Under current home densities, estimated net population growth indicated that the study area was a strong population sink, with negative population growth occurring in nature reserves because of elevation constraints and on private lands because of land-use constraints (Table 1). Net growth of the yellow warbler population was positive only on public lands at mid-elevations, where elevation constraints were intermediate and home densities were low. When the home effect was removed to simulate presettlement conditions, the study area was projected to be a strong population source area, with negative population growth only in the high-elevation nature reserves. These findings suggest that in presettlement times, emigrants from low-elevation source areas were required to maintain a subpopulation of yellow warblers in YNP.

Table 1. Simulated population dynamics of yellow warblers in the study area with and without the influence of rural residences.

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

In sum, the results indicated that levels of bird species richness and abundance were high only in the small portion of the landscape where biophysical factors were favorable. Because nature reserves in the study area were at higher elevations, avian hot spots were primarily outside of reserves, with the majority located on or near private lands. Nature reserves appeared to be population sinks for the yellow warbler, and possibly for the American robin, because of climatic limitations. Low-elevation hot spots were a strong population source area for the American robin because of their more favorable climate. Land use was more intense near low-elevation hot spots, however, and possibly converted population source areas to population sinks for species that are sensitive to the biotic changes associated with RRD, such as the yellow

warbler. Consequently, development on private lands might have reduced the viability of subpopulations at higher elevations in nature reserves.

The yellow warbler is a common species across North America. We selected it for study because its abundance and behavior allowed us to find many nests and to estimate reproductive rates, a task that is very difficult at broad spatial scales. The results for this species are important in that they suggest a mechanism whereby development outside nature reserves may reduce species viability within reserves. This mechanism may apply to other species or subspecies subject to local extinction (within YNP) or to global extinction.

Implications for other species. Like the yellow warbler, several other wildlife species that are commonly seen in YNP may not be able to persist there without access to habitats outside the park (Hansen and Rotella 2002). Because the park is located in the mountainous portion of the ecosystem, it may not provide enough of the lowland habitat required by some species. Species dependent upon lowland riparian woodlands may be especially vulnerable. Within the Montana and Wyoming portion of GYE, we found that 57% of the deciduous forest below 2000 meters was within 2 km of a house by 1997. Among birds, the yellow warbler was one of 16 species that we found only in hot-spot habitats. We were able to monitor nests of 12 of these species and found that, on average, 35% of the nests were parasitized by cowbirds in lowland habitats. These species may be at risk in YNP as lowland habitats are increasingly developed for human use (Hansen et al. 1999). Among these species is the willow flycatcher (*Empidonax traillii*), whose population has been declining significantly in the western United States and which is listed as endangered in the Southwest. Another rare bird species dependent upon aquatic and riparian habitats in GYE is the trumpeter swan (*Cygnus buccinator*). Although this species was hunted to near extinction by the early 1900s, a small population was able to persist in GYE. Current reproductive rates for the trumpeter swan in GYE suggest that lowland habitats are crucial to the recovery of the species in the ecosystem. Several species of butterflies, amphibians, and mammals are found primarily in riparian woodlands (Debinski et al. 1999, Oechsli 2000) in GYE. The effects of intensified land use in low-lying riparian areas on the viability of these organisms has not yet been examined.

A mammal at risk of extinction in YNP is the pronghorn antelope (Yellowstone National Park 1997). This grassland species historically migrated between highland summer habitats within the park and essential lowland winter habitats in Yellowstone Valley. Although protected in the park, the population has declined substantially in the past decade, to about 200 individuals. Scientists speculate that farming and RRD in low-elevation habitats have favored coyotes and other predators, producing high mortality rates among antelope when the herd is in the winter range.

Though not dependent upon lowland habitats, the threatened grizzly bear also appears to face high mortality rates on private lands. As the population of this species recovers in YNP under the protection of the Endangered Species Act, bears are more frequently observed on private holdings in lowlands, where they are killed as a consequence of encounters with hunters and home owners. In and around the Glacier Park–Bob Marshall Wilderness complex in Montana, federal biologists report that more than 60% of conflicts between grizzlies and humans occur on private lands, even though such lands represent only 17% of the region (Chris Servheen [US Department of the Interior grizzly bear recovery coordinator], personal communication, 21 September 2001). Overall rates of human-induced mortality of grizzlies in the northern Rockies have grown in each of the last 3 years to record levels. Many conservationists argue that higher human population densities on private lands threaten the recovery of this species.

Even fish have been at risk from human impacts in lowland streams. In presettlement times, native west-slope cutthroat trout (*Oncochynchus darki lewisi*) and Montana grayling (*Thymallus arcticus montanus*) lived throughout GYE, from headwaters down to major rivers (Varley and Schullery 1998). Subpopulations in headwaters may have been dependent on source populations in lowlands. Mainstream populations were forced to extinction by the introduction of exotic trout species and possibly by habitat changes associated with irrigation and other intense land uses. Headwater subpopulations of grayling also went extinct, even in YNP. (They have since been reintroduced.) West-slope cutthroat persist in headwater streams, but many subpopulations have a high probability of extinction, likely because they no longer receive immigrants from source populations in lowland streams (Shepard et al. 1997).

In sum, our studies of birds, including the yellow warbler, provide evidence of the complex effects on wildlife population dynamics that may result from development on private lands. Such interactions may explain the extinction or near extinction of various species in YNP in the past. Future reduction of native habitats on private lands may further threaten wildlife populations in GYE.

Sustaining human and ecological communities in GYE

The present study suggests that communities in GYE are shifting from an Old West to a New West society and economy. Most of the GYE counties that still depend upon traditional resource extraction industries are nearly stagnant both economically and in terms of population growth. In contrast, those counties that feature high levels of natural amenities and socioeconomic traits associated with the new economy are among the fastest growing in the country. These trends suggest that maintaining the quality of natural amenities may promote economic growth in the region. At the same time, many residents are concerned that the growing population, rural sprawl, and high levels of outdoor recreation are degrading these natural amenities and impeding future economic

expansion. A crucial challenge facing the New West, then, is how to manage land use in a way that sustains local human communities as well as the ecosystems on which they depend (Clark and Minta 1992).

Conservationists have long emphasized that logging, grazing, and mining have harmed biodiversity and ecosystem health in the West. Our results suggest that the newcomers attracted to the West by its natural amenities may also be affecting wildlife through their choices about where to live and play. We have reviewed the evidence that RRD is altering natural habitats, favoring some wildlife species and reducing the population viability of other wildlife species and increasing the mortality rates of threatened species such as the grizzly bear. Studies of the effects of outdoor recreation on wildlife have not been done in GYE, but initial studies in Colorado suggest strong potential impacts (Miller et al. 1998). There is also concern that RRD is altering ecological processes in GYE. The important role of wildfire in ecosystem health is widely recognized in GYE (Romme and Despain 1989). However, land managers are increasingly reluctant to allow naturally occurring fires to burn on public lands because of the risk to homes in the forest. Also, exotic weeds and diseases increasingly threaten wildlife forage and fish populations in GYE (Varley and Schullery 1997). The spread of these invasive species may be enhanced by RRD and outdoor recreation (Marcus et al. 1998). Just as Americans “mined” the Old West through logging, livestock grazing, and mining (Wilkinson 1993), they might be mining the New West through rural sprawl and extravagant recreational activity.

One implication of our study is that national parks, wilderness areas, and other nature reserves are facing a new set of threats in the New West. The people who are attracted to the lands surrounding the reserves may be shrinking the natural buffers of those reserves and altering the ecosystems within them. National parks are less and less the “vignettes of primitive America” envisioned by Aldo Leopold (Boyce 1998); rather, they are becoming islands of seminatural habitat increasingly altered by the press of humanity around and within them. Managers of these reserves face the very difficult challenge of maintaining ecological processes and native species in the face of the conflicting—even, at times, internally contradictory—wants and needs of the people who live and work in the New West.

A second implication of this study is that local communities may best be able to promote economic growth by maintaining the natural amenities that are so attractive to new residents and businesses. If this is true, policies that favor timber harvesting over scenery, mining over water quality, or intensive livestock grazing over wildlife habitat might actually inhibit rather than expand economic growth. Rather, GYE counties that wish to stimulate economic growth may find it prudent to expand wilderness areas and other public lands, manage land use to protect scenery, ensure that streams and rivers remain free flowing, and conserve wildlife.

The current understanding of the influence of natural amenities on economics is underdeveloped, however. The

specific features of the environment that attract economic development are poorly understood. What are the relative contributions of scenery, outdoor recreation, climate, wildlife, rural living, and low levels of traffic congestion to the appeal of an area? To what extent can some or all of these factors be degraded without rendering an area unattractive? If the large cities of the United States become increasingly unlivable, will rural areas remain relatively attractive even if the natural amenities are substantially degraded? Once a region with high levels of natural amenities grows above a threshold population size, will infrastructure and socioeconomic factors drive continued population growth and economic expansion, regardless of natural amenities?

Clearly, more research is needed on how to retain healthy ecosystems and livable human communities in the New West. Based on current knowledge, however, we suggest that several strategies will help bring about sustainability:

- *Improving understanding of the interactions between ecosystems and economics.* Well-founded information on the economic and ecological consequences of alternative policy approaches is largely lacking in GYE and throughout the West. Objective research is needed on the relative merits of various resource extraction and natural amenity policies for achieving public and private goals.
- *Integrating assessment and management of public and private lands.* Currently, GYE lands are managed within administrative boundaries that correspond poorly to ecological boundaries. Consequently, management plans are often costly and ineffective. New paradigms in land management are needed that lead to assessments and policies organized around and across ecological boundaries and that consider the differing objectives of management jurisdictions. A successful example in the Montana portion of GYE is the cooperative management of elk across the federal, state, and private lands that comprise high-elevation summer and low-elevation winter habitats (Schullery 1997).
- *Developing and using decision-support tools for land management.* Rapid-assessment field studies, remote sensing, geographic information systems, and computer simulation models are powerful tools for landscape assessment and management. These can be used to assess past change and project likely change under alternative management scenarios. Unfortunately, many state agencies and local governments do not have access to such tools because they lack funds or have insufficient technical expertise, or both. Cooperative programs are needed to enable federal, state, and local agencies to share in the development and use of such decision-support tools.
- *Making land-use designations on the basis of ecological and socioeconomic goals.* Sound human judgment and decision-support tools should be used to identify the places in the landscape that would be best suited to

either ecological or socioeconomic objectives. Local governments could then use this information in deciding where to place green space, subdivisions, and commercial activities. Our analysis indicates, for example, that protecting avian "hot spots" (which cover only 2.7% of the study area) could significantly advance biodiversity goals. Sound land-use guidance is also needed by environmental trusts and other organizations that are protecting lands through acquisition or conservation easements. Also, the Conservation Reserve Program could be expanded to intentionally protect agricultural lands that are important to biodiversity.

- *Educating the public.* Many home owners, realtors, and recreationists are poorly informed about the ecological consequences of their daily decisions. Rather than assume that public lands and land managers alone can fully protect ecosystems, all citizens need to share in the pursuit of community goals. Education programs are desperately needed to teach citizens how to live more lightly on the land. Similarly, elected officials would benefit from training on the options available for growth management, including conservation easements, citizen-driven planning, zoning, and public finance measures; the fiscal impacts of various forms of development and land use; and integration of scientific information into growth management plans.

To varying degrees, each of these sustainability strategies is now being implemented in GYE. However, with the rapid rate of population growth and the intensification of land use, options for implementing sustainable management approaches are quickly being foreclosed. The continuation of current trends will very likely reduce the ecosystem qualities that most Americans assume are fully protected in YNP, the nation's first national park. Learning how to sustain GYE will bring benefits that extend far beyond that region. With many of the world's nature reserves under assault from human expansion onto surrounding lands (Hansen and Rotella 2001), answers for GYE may help guide more sustainable development elsewhere on the planet.

Acknowledgments

We thank the numerous field and laboratory technicians who helped to collect the data summarized in this article. Several private landowners and government agencies granted permission to conduct research on their holdings, including Yellowstone National Park, Gallatin National Forest, Targhee National Forest, Red Rock Lakes National Wildlife Refuge, and the Montana Department of Fish, Wildlife and Parks. Data were provided by Yellowstone National Park; the Shoshone, Gallatin, and Targhee National Forests; the US Geological Survey Rocky Mountain Science Center; and the 20 GYE counties. Our research was supported by the National Aeronautics and Space Administration's Land Cover/Land Use Change Program; the US Department of Agriculture Research, Education, and Extension Competitive Grants Program; the Montana Department of Fish, Wildlife and Parks; the National Fish and Wildlife Foundation; and the US Fish and Wildlife Service.

We also thank Matthew Greenstone, F. Swanson, D. Glick, and two anonymous reviewers for helpful comments on the manuscript.

References cited

- Beale CL, Johnson KM. 1998. The identification of recreation counties in non-metropolitan areas of the USA. *Population Research and Policy Review* 17:37–53.
- Beyers WB, Nelson PB. 2000. Contemporary development forces in the nonmetropolitan West: New insights from rapidly growing communities. *Journal of Rural Studies* 16: 459–474.
- Boyce MS. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. *Wildlife Society Bulletin* 26: 391–398.
- Brooks T, Balmford A, Burgess N, Fjelds J, Hansen LA, Moore J, Rahbek C, Williams P. 2001. Toward a blueprint for conservation in Africa. *BioScience* 51:613–624.
- Clark TW, Minta SC. 1992. Greater Yellowstone's Future: Prospects for Ecosystem Science, Management, and Policy. Washington (DC): Island Press.
- Craighead JJ. 1991. Yellowstone in transition. Pages 27–40 in Kieter RB, Boyce MS, eds. *The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage*. New Haven (CT): Yale University Press.
- Cromartie JB, Wardwell JM. 1999. Migrants settling far and wide in the rural West. *Rural Development Perspectives* 14: 2–8.
- Debinski DM, Jakubauskas ME, Kindscher K. 1999. A remote sensing and GIS-based model of habitats and biodiversity in the Greater Yellowstone Ecosystem. *International Journal of Remote Sensing* 20: 3281–3292.
- Despain D. 1990. Yellowstone Vegetation. Boulder (CO): Roberts Rinehart.
- Goldstein B. 1992. The struggle over ecosystem management at Yellowstone. *BioScience* 42: 183–187.
- Hansen AJ, Rotella JJ. 2001. Nature reserves and land use: Implications of the “place” principle. Pages 57–75 in Dale V, Haeuber R, eds. *Applying Ecological Principles to Land Management*. New York: Springer-Verlag.
- . 2002. Biophysical factors, land use, and species viability in and around nature reserves. *Conservation Biology*. Forthcoming.
- Hansen AJ, Rotella JJ, Kraska ML. 1999. Dynamic habitat and population analysis: A filtering approach to resolve the biodiversity manager's dilemma. *Ecological Applications* 9: 1459–1476.
- Hansen AJ, Rotella JJ, Kraska ML, Brown D. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. *Landscape Ecology* 15:505–522.
- Ingram K, Lewandrowski J. 1999. Wildlife conservation and economic development in the West. *Rural Development Perspectives* 14: 44–51.
- Johnson JD, Rasker R. 1995. The role of economic and quality of life values in rural business location. *Journal of Rural Studies* 11: 405–416.
- Johnson KM. 1998. Renewed population growth in rural America. *Research in Rural Sociology and Development* 7: 23–45.
- Laitos JG, Carr TA. 1999. The transformation on public lands. *Ecology Law Quarterly* 26: 140–242.
- Levitt J, ed. 2002. *Conservation in the Internet Age*. Washington (DC): Island Press.
- Marcus A, Milner GM, Maxwell BD. 1998. The distribution of spotted knapweed (*Centaurea maculosa*) in the Bitterroot Selway Wilderness high-use areas. *Great Basin Naturalist* 58: 156–166.
- Marzluff JM, Bowman R, Donnelly R. 2001. A historical perspective on urban bird research: Trends, terms and approaches. Pages 1–17 in Marzluff JM, Bowman R, Donnelly R, eds. *Avian Ecology and Conservation in an Urbanizing World*. Boston: Kluwer Academic.
- McGranahan DA. 1999. *Natural Amenities Drive Population Change*. Washington (DC): Food and Rural Economics Division, Economic Research Service, US Department of Agriculture.
- Miller SG, Knight RL, Miller CK. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8: 162–169.
- Nelson PB. 1999. Quality of life, nontraditional income, and economic growth. *Rural Development Perspectives* 14: 32–37.
- Oechsli LM. 2000. *Ex-urban Development in the Rocky Mountain West: Consequences for Native Vegetation, Wildlife Diversity, and Land-Use Planning in Big Sky, Montana*. Master's thesis. Montana State University, Bozeman, MT.
- Power TM. 1991. Ecosystem preservation and the economy of the Greater Yellowstone area. *Conservation Biology* 5: 395–404.
- . 1998. *Lost Landscapes and Failed Economies: The Search for a Value of Place*. Washington (DC): Island Press.
- Rasker R. 1991. Dynamic economy versus static policy in the Greater Yellowstone Ecosystem. In *Proceedings of the Conference on the Economic Value of Wilderness*; 8–11 May 1999; Jackson, Wyoming. Asheville (NC): Southeastern Forest Experiment Station, US Forest Service.
- Rasker R. 1993. Rural development, conservation and public policy in the Greater Yellowstone Ecosystem. *Society and Natural Resources* 6: 109–126.
- Rasker R, Glick D. 1994. The footloose entrepreneurs: Pioneers of the New West? *Illiahee* 10: 34–43.
- Rasker R, Hansen AJ. 2000. Natural amenities and population growth in the Greater Yellowstone region. *Human Ecology Review* 7: 30–40.
- Riebsame WE, Gosnell H, Theobald D, eds. 1997. *Atlas of the New West*. New York: W. W. Norton.
- Rodman A, Shovic H, Thoma D. 1996. *Soils of Yellowstone National Park. Yellowstone National Park (WY): Yellowstone Center for Resources. Report no. YCR-NRSR-96-2.*
- Romme WH, Despain DG. 1989. Historical perspective on the Yellowstone fires of 1988. *BioScience* 39: 695–699.
- Rotella JJ, Taper ML, Hansen AJ. 2000. Correcting nesting-success estimates for observer effects: Maximum-likelihood estimates of daily survival rates with reduced bias. *The Auk* 11: 92–109.
- Rudzitis G. 1999. Amenities increasingly draw people to the rural West. *Rural Development Perspectives* 14: 9–13.
- Rudzitis G, Johansen HE. 1991. How important is wilderness: Results from a United States survey. *Environmental Management* 15: 227–233.
- SAS Institute. 1996. *SAS/STAT changes and enhancements through version 6.12*. Cary (NC): SAS Institute.
- Schullery P. 1997. *Searching for Yellowstone*. Boston: Houghton Mifflin.
- Shepard BB, Sanborn B, Ulmer L, Lee DC. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River Basin, Montana. *North American Journal of Fisheries Management* 17:1158–1172.
- Theobald DM. 2000. Fragmentation by inholdings and exurban development. Pages 155–174 in Knight RL, Smith FW, Buskirk SW, Romme WH, Baker WL, eds. *Forest Fragmentation in the Central Rocky Mountains*. Boulder: University Press of Colorado.
- Varley JD, Schullery PD. 1998. *Yellowstone Fishes: Ecology, History, and Angling in the Park*. New York: Stackpole Books.
- Wilkinson CF. 1993. *Crossing the Next Meridian: Land, Water, and the Future of the West*. Washington (DC): Island Press.
- Yellowstone National Park. 1997. *Yellowstone's Northern Range: Complexity and Change in a Wildland Ecosystem*. Mammoth Hot Springs (WY): National Park Service.