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Source: Wildlife Biology, 18(3) : 246-257

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/11-060

Wildl. Biol. 18: 246-257 (2012)
DOI: 10.2981/11-060

www.wildlifebiology.com

Original article

Impacts of rural development on Yellowstone wildlife: linking grizzly bear *Ursus arctos* demographics with projected residential growth

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Exurban development is consuming wildlife habitat within the Greater Yellowstone Ecosystem with potential consequences to the long-term conservation of grizzly bears *Ursus arctos*. We assessed the impacts of alternative future land-use scenarios by linking an existing regression-based simulation model predicting rural development with a spatially explicit model that predicted bear survival. Using demographic criteria that predict population trajectory, we portioned habitats into either source or sink, and projected the loss of source habitat associated with four different build out (new home construction) scenarios through 2020. Under boom growth, we predicted that 12 km^2 of source habitat were converted to sink habitat within the Grizzly Bear Recovery Zone (RZ), 189 km^2 were converted within the current distribution of grizzly bears outside of the RZ, and 289 km^2 were converted in the area outside the RZ identified as suitable grizzly bear habitat. Our findings showed that extremely low densities of residential development created sink habitats. We suggest that tools, such as those outlined in this article, in addition to zoning and subdivision regulation may prove more practical, and the most effective means of retaining large areas of undeveloped land and conserving grizzly bear source habitat will likely require a landscape-scale approach. We recommend a focus on land conservation efforts that retain open space (easements, purchases and trades) coupled with the implementation of 'bear community programmes' on an ecosystem wide basis in an effort to minimize human-bear conflicts, minimize management-related bear mortalities associated with preventable conflicts and to safeguard human communities. Our approach has application to other species and areas, and it has illustrated how spatially explicit demographic models can be combined with models predicting land-use change to help focus conservation priorities.

Key words: Greater Yellowstone Ecosystem, grizzly bears, landscape planning, land-use change, rural development, Ursus arctos

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Received 13 July 2011, accepted 9 March 2012

Associate Editor: Stephanie Kramer-Schadt

Grizzly bears *Ursus arctos* are considered wilderness species requiring large undisturbed areas (Craighead et al. 1995). Historically, grizzly bears in North America ranged from Alaska to Mexico and California to the Dakotas, occupying numerous ecosystems. However, most grizzly bear populations currently occur in close proximity to humans and are considered conservation-reliant (Scott et al. 2005). Maintaining viability of these populations is a challenge for wildlife managers. In the continental United States, grizzly bears are listed as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1993). The Yellowstone grizzly bear was delisted in April 2007 (U.S. Fish and Wildlife Service 2007b), but relisted by court order in November 2009, a decision currently under appeal.

In British Columbia, Canada, there are concerns about long-term consequences of human changes to landscapes and the continued health of grizzly bear populations (Herrero 2005). The Alberta grizzly bear was formally listed by the province as threatened in June 2010 (Festa-Bianchet 2010). Few places exist where human land-use development has not adversely impacted grizzly bear habitats.

Long-term conservation of grizzly bears is directly related to human activity. This proximity between bears and humans has resulted in a source-sink dynamic (Knight et al. 1988, Schwartz et al. 2006e, Schwartz et al. 2010) in the Greater Yellowstone Ecosystem (GYE) where bears die at higher rates in and adjacent to areas with human activities. Schwartz et al. (2010) demonstrated that grizzly bear survival was negatively associated with increases in roads, human residences, other developed sites (e.g. campgrounds and lodges) and the time bears used areas open to ungulate hunting.

Rapidly accelerating growth of rural residential development (i.e. exurban sprawl) in some areas in Montana, Idaho and Wyoming has been identified as a factor impacting bear habitat (Schwartz et al. 2010) with the potential for an increase in grizzly bear-human conflicts and bear mortalities.

Human population growth in the Mountain West has exceeded growth in the rest of the nation. During 1970-1999, the GYE experienced a 58% increase in population size and a 350% increase in the area of rural land development (Gude et al. 2006). Land development exceeded population growth due to low-density (1 home/0.4-16.2 ha) exurban development (Gude et al. 2006). Gude et al. (2007) estimated that in 1980, about 3.1% of occupied grizzly bear habitat (Schwartz et al. 2002) had been impacted by exurban development, but projected that by 2020, 6.9% would likely be impacted under aggressive growth management and 10.7% under the boom growth scenario. In their biodiversity assessment of alternative future scenarios, Gude et al. (2007) did not estimate resulting changes in survival or reproduction of specific wildlife populations. Although other studies have done this (White et al. 1997, Schumaker et al. 2004), they felt that this step should be undertaken when sufficient data allowed for meaningful predictions. As a consequence, although the approach used by Gude et al. (2007) provided insight into the potential consequences of exurban development on grizzly bears, it did not quantify impacts to grizzly bear demographics. Additionally, bear numbers and bear distribution have continued to increase in the GYE, necessitating the need for a more rigorous analysis.

Here we build on Gude et al. (2007) and demonstrate how the distribution and extent of grizzly bear source and sink habitats may change under forecasted residential development scenarios. We define source habitats as those areas in the landscape within occupied grizzly bear range where predicted adult female survival was ≥ 0.91. We could have used a different rate, but chose 0.91 because Harris et al. (2006) demonstrated that with current GYE rates of reproduction (0.318 female cubs/female/year; Schwartz et al. 2006a) and survival of dependent young (cubs = 0.63 and yearlings = 0.817; Schwartz et al. 2006d), lambda (λ) ≥ 1.0 in 95% of stochastic simulations when adult female survival was 0.91. Schwartz et al. (2010) used this break point in female survival to illustrate the spatial extent of source and sink habitats in the GYE. In this article, we build on those projections and illustrate the spatial extent of increased sink habitats in the GYE associated with four projected build out scenarios developed by Gude et al. (2007). Our approach has application to other species and areas and illustrated how spatially explicit demographic models can be combined with models predicting land-use change to help focus conservation priorities.

Study area

Grizzly bears currently occupy approximately 37,200 km^2 in the GYE (Schwartz et al. 2006b; Fig. 1) including Yellowstone and Grand Teton National Parks, portions of six adjacent national forests, plus state and private lands in Montana, Wyoming and Idaho. The GYE is a high-elevation plateau with 14 surrounding mountain ranges with elevations $>$ 2,130 m a.s.l., and it contains the headwaters of three major continental-scale rivers. Summers are short with most average annual precipitation (50.8 cm) falling as snow. Vegetation varies from low-elevation grasslands through conifer forests at mid-elevations, reaching alpine tundra around 2,900 m a.s.l. Detailed descriptions of the geography, climate and vegetation appear in Schwartz et al. (2006c).

For purposes of his research, Rasker (1991) expanded the definition of the GYE to include the 20 surrounding counties because of the strong ecological and socio-economic linkages between public and private lands within the area. Gude et al. (2007) used this area because development regu-

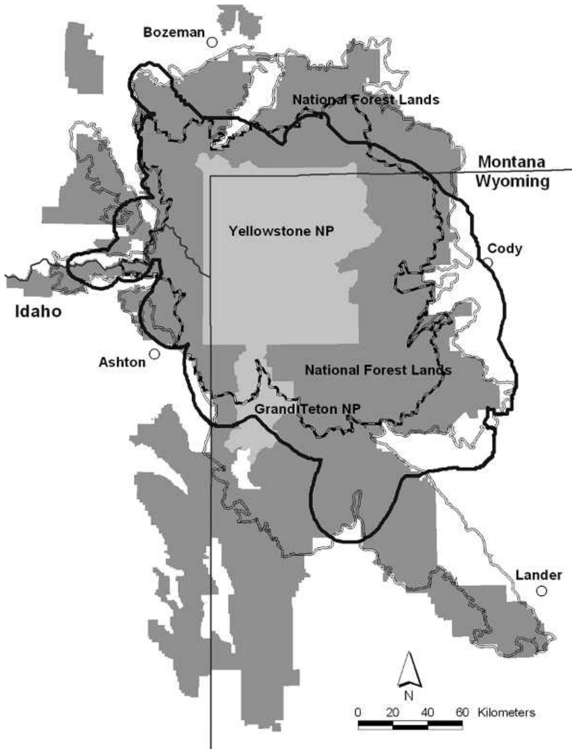

Figure 1. The Greater Yellowstone Ecosystem with Forest Service (dark grey) and National Park (light grey) lands displayed. The U.S. Fish and Wildlife Service (FWS) Grizzly Bear Recovery Zone is shown by the dashed line, the current distribution of grizzly bears by the heavy black line, and the area identified as suitable grizzly bear habitat by the FWS by the open line. Bears have recolonized some historic range beyond suitable habitat identified by the FWS.

lations and growth management were implemented at the county level. The area encompassed 145,635 km^2 with public and tribal lands making up 68% of the region. Land ownership was divided among private lands (32%), USDA Forest Service (32%), USDI Bureau of Land Management (19%), USDI National Park Service (7%), Tribal Lands (5%), and state lands, wildlife refuges and other federal lands (5%; Gude et al. 2007).

Methods

Rural residential development

We used future exurban build out scenarios of Gude et al. (2007) to evaluate the potential impacts on grizzly bear survival and changes in the amounts of source habitat. Gude et al. (2007) used an existing regression-based simulation model (Table 1) to project alternative growth scenarios of future rural home development. This simulation model was based on regression and forecasted development, with a measured degree of confidence, based on rates of development during the 1990s and regional covariates including transportation infrastructure, natural amenities and existing development (Gude et al. 2007). The road density variable described kilometers of all roads per square kilometer. We calculated the airport travel time variable by using cost-distance grid functions incorporating distance and automobile speed limits. The development indicator was a binary variable describing whether or not each section (section = 1 square mile, 2.59 km^2) contained any homes prior to 1990. Other past-development indicators included the number of rural homes present prior to 1990 within a 1-section and 20-section radius. We calculated proximity to forested areas using travel time, and proximity to rivers and streams was calculated as Euclidian distance.

We chose this simulation method over other approaches because of its statistical approach, comprehensive accuracy assessment and ability to generate scenarios based on alternative land-use policies. The method modeled the path of growth over time and was calibrated to and validated against historical development patterns (Gude et al. 2007). We used four of their growth scenarios: status quo, low, boom and aggressive growth management. The low-growth, status quo and boom scenarios forecast growth under existing land-use policies. The aggressive growth management scenario implemented hypothetical growth management policies designed to direct growth away from biodiversity elements most at risk of development pressure under the status quo future growth scenario. These models projected growth until 2020, and we contrasted those projections to existing conditions in 1999.

To evaluate the potential impact of exurban growth on grizzly bears, we used a model from Schwartz et al. (2010) to predict adult female grizzly bear survival at the 30 m^2 pixel scale across the landscape in 1999 and projected changes under the four growth scenarios. Schwartz et al. (2010) used the known fate data type in Program MARK (White & Burnham 1999) to estimate mean survival and investigate influences of various covariates on grizzly bear survival. The known fate model employed binomial likelihood functions over monthly intervals (White & Burnham 1999). The technique applied maximum likelihood theory to estimate survival rates, used the information-theoretic method for model selection and multi-model inferences (Burnham & Anderson 2002), and evaluated the effect of

Table 1. Coefficient estimates, confidence intervals and significant levels described for parameters of the best model of growth in rural residential development during the 1990s. Data from Gude et al. (2007).

Model parameters	β	95% CL	P
Intercept	9.02	7.39 - 10.73	< 0.0001
Road density	3.01	2.53 - 3.49	< 0.0001
Airport travel time	-0.65	-0.98 - -0.34	< 0.0001
Development indicator	1.75	1.65 - 1.86	< 0.0001
Homes in 1-section radius	3.80	3.12 - 4.52	< 0.0001
Homes in 20-section radius	0.16	0.03 - 0.30	< 0.0203
Homes in 20-section radius, quadratic term	-0.89	-1.12 - -0.66	< 0.0001
Construction during previous decade	9.76	8.14 - 11.47	< 0.0001
Streams/rivers proximity	-1.12	-1.33 - -0.92	< 0.0001
Forest areas travel time	-3.31	-3.58 - -3.03	< 0.0001
Dispersion	3.67	3.46 - 3.89	

temporal, individual and spatial covariates on annual survival rates. We assigned spatial covariates individually to each bear based upon its telemetry locations.

The best model of Schwartz et al. (2010) included explanatory covariates that predicted bear survival in a spatial context of sex, circumstance of capture, season, road density, housing density, number of developed sites, amount of secure habitat, whether the area was open to autumn hunting for ungulates and elevation. Predicted survival was greater for females than males. Because grizzly bear demographics are largely driven by adult female survival (Harris et al. 2006), we only focus on females here. Circumstances of capture were predictive of survival with managed bears (those getting into trouble with humans) experiencing greater rates of mortality. Because we were interested in evaluating the impacts of rural residential development on the bear population as a whole, we focussed on what Schwartz et al. (2006c, 2010) refer to as their study sample. The winter (November-March) season was treated as a temporal covariate in their model because bear mortality was nearly zero when they were in dens (Haroldson et al. 2006). The spring/summer (April-July) and autumn (August-October) seasons were treated separately, with spatial covariates coded to each season. Results of the model demonstrated that as road density increased, predicted survival declined. Road density was measured within a 0.25 km^2 moving window. Bears living in roadless areas had higher predicted survival. Roadless areas (i.e. secure habitat) were defined as any area $\geq$ 4.05 ha (10 acres) $>$ 500 m from an open or gated road. As residential homes increased, predicted grizzly bear survival declined. Schwartz et al. (2010) compared the total count of homes/2.59 km^2 against the natural log (count of homes + 1) of total homes hypothesizing that the effect of change from one to two homes was much greater on bear survival than changing, for example, from 101 to 102 homes. The natural log was a more predictive covariate and appeared in their top model. We used it here to forecast changes in the rural residential build out scenarios of Gude et al. (2007). Survival was predicted to decline as the number of developed sites (e.g. lodges, camp grounds and cabins) within a bear's home range increased. As elevation increased, bear survival also increased. Finally, bears using areas open to fall ungulate hunting had lower predicted levels of survival than bears residing inside areas closed to hunting (i.e. national parks).

When we contrasted the build out scenarios of Gude et al. (2007), we held all covariates in the top model of Schwartz et al. (2010) at their 1999 levels and only adjusted home and road density projected to occur within each 2.59 km^2 pixel. We contrasted build out scenarios in three different zones: 1) the Grizzly Bear Recovery Zone (U.S. Fish and Wildlife Service 1993), 2) within the known distribution of grizzly bears (Schwartz et al. 2006b), and 3) within suitable grizzly bear habitat identified by the Fish and Wildlife Service (U.S. Fish and Wildlife Service 2007a). We chose to illustrate results using a deterministic approach, and did not focus on issues of uncertainty. We recognize that uncertainty must be addressed but agree with Beissinger & Westphal (1998) that uncertainty is not an excuse for not making a management decision.

The Final Conservation Strategy (U.S. Fish and Wildlife Service 2007a), a document that directed population and habitat monitoring and management activities for the GYE grizzly bear post delisting, stipulated no net change in the number of developed sites on public lands within the Primary Conservation Area (PCA). The PCA coincides with the designated U.S. Fish and Wildlife Service Recovery Zone. Even though the bear was relisted by a court order in 2009, the agencies continue to follow recommendations in the Strategy. Here, we considered projected residential development on private lands.

Results

Because, grizzly bear survival was quite sensitive to increased residential home density, the model of Schwartz et al. (2010) predicted that survival dropped below 0.91 once a home appeared within a section without considering associated increase in road density. Consequently, build out scenarios effectively changed source habitats without homes to sink habitats once a new house was projected to be developed. As expected, the boom growth scenario resulted in a higher percentage of source habitat being converted to sink habitat (Table 2). In the boom scenario, 12 km^2 of source habitat were converted to sink habitat within the PCA, 189 km^2 were converted within the current distribution of grizzly bears outside of the PCA, and 289 km^2 were converted in the area outside the PCA identified as suitable grizzly bear habitat by the U.S. Fish and Wildlife Service (Fig. 2). The largest percent change occurred on private lands within the PCA (-11.5%) followed by suitable habitat (-4.8%), and finally within occupied grizzly bear habitat (-3.3%; see Table 2). Overall maintenance of the status quo trend in development resulted in the second greatest decline in source habitat whereas the growth management resulted in the least change outside the PCA. Areas

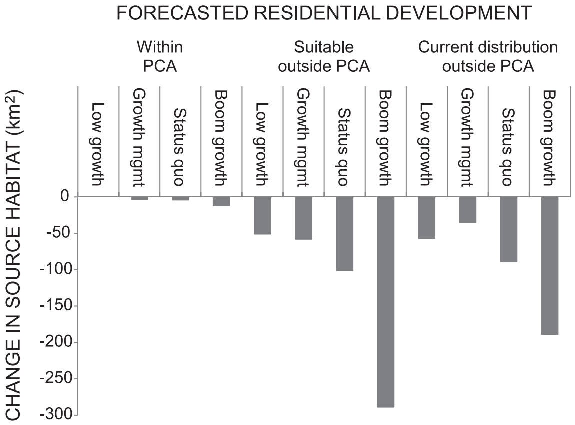

Figure 2. Change in the area (km^2) of private land that is source habitat between forecasted residential development scenarios within the Primary Conservation Area (PCA), outside the PCA and within defined suitable grizzly bear habitat, and outside the PCA and within the current distribution of grizzly bears, Greater Yellowstone Ecosystem, Montana, Idaho and Wyoming, USA.

projected to have the greatest amount of source habitat converted to sink habitat as a result of exurban development were the Big Sky-Moonlight Basin areas east of Ennis, Montana, the area around Henrys Lake near Island Park, Idaho, an area north of Jackson Hole, Wyoming, and the areas west of Cody, Wyoming including the North Fork and South Fork of the Shoshone River (Fig. 3). Much of the remaining development was projected to occur outside existing grizzly bear habitat in areas already developed.

Discussion

The methods we used illustrate how models addressing wildlife demographics and human land-use development can be combined to spatially identify lands with potential conservation concerns. The

Table 2. Area (km^2) of public and private lands within the Primary Conservation Area (PCA) and outside the PCA within defined suitable grizzly bear habitat, and within the current distribution of grizzly bears outside the PCA. The percentage change in source habitat to sink habitat is also shown based on build out scenarios, Greater Yellowstone Ecosystem, Montana, Wyoming and Idaho, USA, 1999-2020.

	Public in PCA			Private in PCA			Suitable out PCA			Distribution out PCA		
Scenario	Sink	Source	Change (%)	Sink	Source	Change (%)	Sink	Source	Change (%)	Sink	Source	Change (%)
Survival 1999	3169	20099	0	99	15	0.0	6008	15736	0.0	5774	7881	0.0
Status quo	3169	20099	0	103	11	-4.0	6108	15635	-1.7	5862	7792	-1.5
Low growth	3169	20099	0	99	15	-0.1	6058	15685	-0.8	5831	7824	-1.0
Growth management	3169	20099	0	102	12	-2.8	6065	15678	-1.0	5808	7846	-0.6
Boom growth	3169	20099	0	111	3	-11.5	6296	15447	-4.8	5962	7692	-3.3

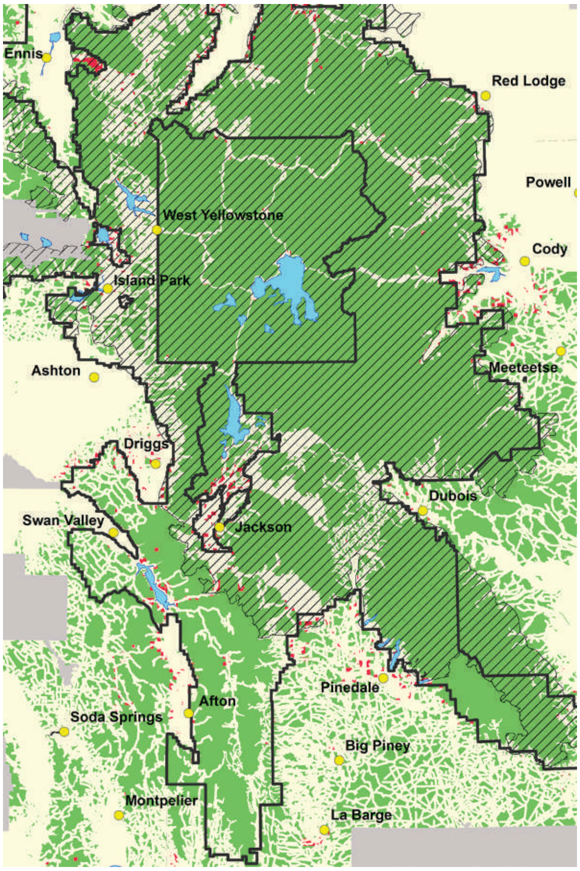

Figure 3. The Greater Yellowstone Ecosystem depicting changes in habitats due to extrapolated urban and exurban boom growth. Areas shown in green represent source habitat for grizzly bears where female survival is predicted to be ≥ 0.91. Sink habitats are shown in cream colour and represent areas where female survival < 0.91. Habitats that changed from source to sink due to projected boom growth are depicted in red. The hatched area represents the area identified as suitable grizzly bear habitat by the U.S. Fish and Wildlife Service. Grey areas represent areas where no data were available.

method has potential application beyond grizzly bears in the GYE. Our model projections demonstrate the likelihood of continued erosion of secure grizzly bear habitat both within the PCA and beyond in occupied and suitable grizzly bear habitat. Projected development in the GYE affected grizzly bear habitat in one of three ways: 1) it fractured areas of secure habitat into smaller and therefore potentially less valuable habitat, 2) it made the human-created edge of where natural habitat ends and the human altered landscape begins more clear (Hilty et al. 2006) or 3) it occurred outside of suitable bear habitat with little consequence to the long-term conservation of bears. Projected development in the Big Sky-Moonlight Basin, Montana area has the potential to fracture currently contiguous, secure grizzly bear habitat. Big Sky-Moonlight Basin are private lands located within occupied grizzly bear habitat east of Madison Valley (Fig. 4). Development in the Big Sky area already constitutes sink habitat and projected development west of Big Sky in the Moonlight Basin could potentially fracture the Lee Metcalf Wilderness to the north from undeveloped forest service lands and the Lee Metcalf Wilderness to the south. Projected development in the Henrys Lake area of Idaho may also create a fracture zone for grizzly bears attempting to move between Forest Service lands west of the continental divide and east of the Henrys Fork with the Centennial Mountains in Montana and Idaho to the west, a possible linkage between the GYE and the Bitterroot Range (Fig. 5). Grizzly bears currently occupy this area and are continuing to move west into the Centennial Mountains east of Interstate Highway 15.

Projected development west of Cody, Wyoming, including the North Fork and South Fork of the Shoshone River, will make the interface between secure grizzly bear habitat and the urban interface adjacent to Cody, Wyoming, more clear. Projected development in the drainage of the river will also add to the already existing fracture zone created by roads and developments in the valley bottoms projecting into secure grizzly bear habitat. This area was first identified as a conflict 'hot-spot' in 2006 (Gunther et al. 2007) and continues to be an area of concern.

The area of developed land in USA increased by 14.2 million ha between 1982 and 2003, and is projected to increase another 22 million ha between 2003 and 2030 (White et al. 2009). Development in the Rocky Mountain region is projected to increase 57% by 2030 (White et al. 2009). The development projections of Gude et al. (2007) were based on growth rates in the 1990s. These rates differ from current growth rates that reflect the economic down turn of the 2000s (Fig. 6) and higher gasoline costs that could increasingly discourage long commutes (Goodman 2008). Consequently, our projections are preliminary and may or may not occur within the next decade and could differ from historic growth rates. However, our projections reflect the most likely spatial locations of future growth and serve to focus conservation planning where development of private lands will likely occur thus maintaining the value of these lands as wildlife habitat.

According to Leu et al. (2008), by 2003, the anthropogenic footprint of human development

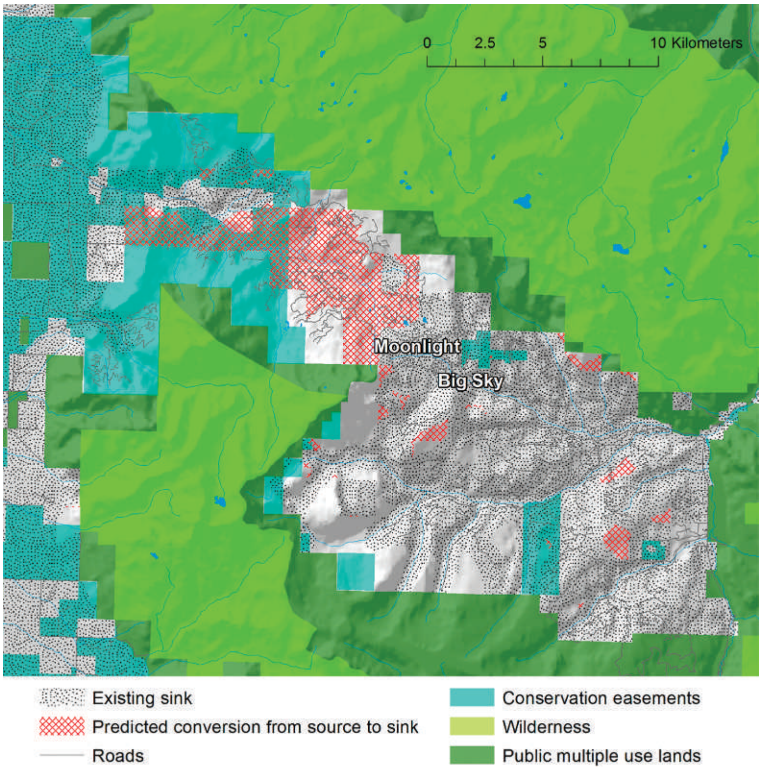

Figure 4. Big Sky-Moonlight Basin, Montana, USA, shows existing sink habitat (grey stipples) and projected conversion of source habitat to sink habitat (red cross hatching) under a boom growth scenario until 2020. Existing and projected exurban development has the potential to restrict travel between two large tracks of Forest Service Wilderness to the north and south (light green). Most conservation easements (shown in blue) allow for a low level of development, and for illustration purposes here, we assume that at least one home could be built per section.

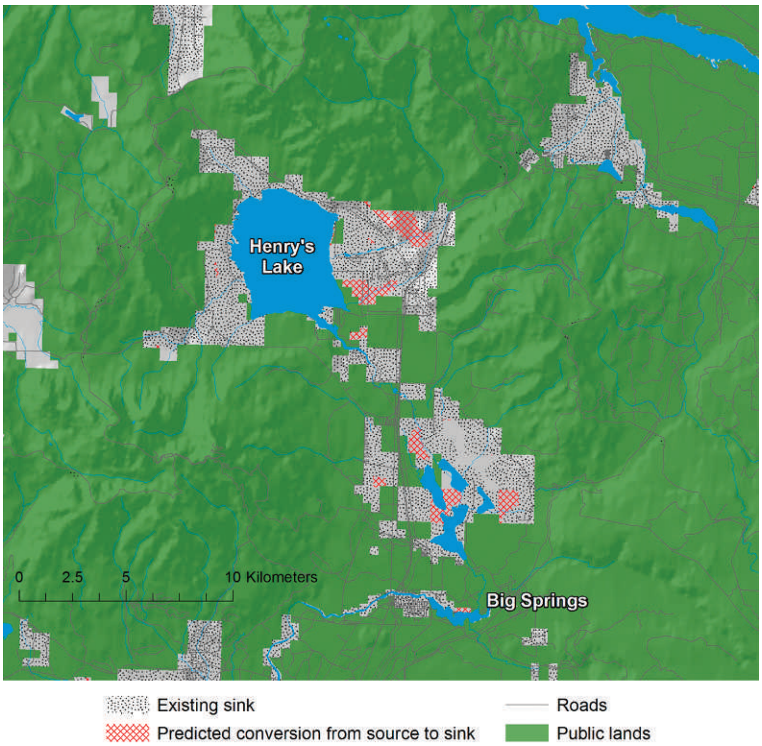

Figure 5. Henrys Lake, Idaho, USA, shows projected development and sink habitat adjacent to the Centennial Mountains. Some of these lands are protected by conservation easements (these data were unavailable to us) but the potential development in the region could fracture or impair linkage between the Targhee National Forest lands west of the continental divide but linkage east of the Henrys Fork and the Centennial Mountains west remains high.

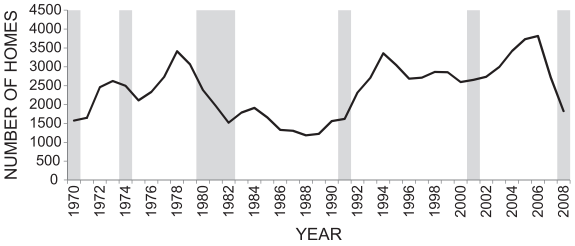

Figure 6. Rural home construction in western Montana, 1970-2008, shown as homes built further than 10 minutes from Billings, Bozeman, Butte, Great Falls, Kalispell and Missoula. Slowdowns in construction coincide with approximate timing of national recessions (grey columns). Data from Headwaters Economics, Bozeman, Montana, USA.

affected about 13% of the area of the western United States with agriculture, populated areas and secondary roads being the three dominate features. However, when viewed at the GYE eco-region (Utah-Wyoming Rocky Mountains, Nature Conservancy 2001), Leu et al. (2008; Fig. 3) estimated that only about 12% of the GYE fell into their human footprint category 1 (minimal human footprint intensity) which represented secure grizzly bear habitat. Leu et al. (2008) also indicated that if the current trajectory of human population expansion in the western United States continues, populated areas will increasingly dominate western landscapes at the expense of ranch and farmland. Exurban developments are converting large landholdings to housing at unprecedented rates, and the effects of such conversions on ecological processes are poorly understood (Knight et al. 1995, Odell & Knight 2001, Theobald 2001, Hansen et al. 2005).

The survival model (Schwartz et al. 2010) we used implicated housing development as a factor reducing grizzly bear survival in the GYE. This model only considered how the number of homes within bear home ranges influenced survival, but did not account for differences in human behaviour, an important variable that the authors could not quantify. Ignoring differences in human behaviour, the model predicted that the construction of a single house within an undeveloped section of land was enough to convert that habitat to a sink for grizzly bears.

Our choice of dividing source and sink habitats based on the point estimate of independent female survival of 0.91 was clearly conservative. As indicated by Harris et al. (2006), lambda was projected to be $\geq$ 1 in 95% of the simulations. Lambda was projected to be $\geq$ 1 in 50% of simulations when female survival was equal to 0.89. Decisions of what value to choose depend upon management concerns for the species and what level of uncertainty is acceptable for management. For simplicity and clarity, we chose to provide point estimates of predicted survival in our build out scenarios and not address issues of sampling uncertainty. We recognize this as an unsolved problem, and our results should therefore be tempered with caution.

Source-sink theory (Pulliam 1988) suggests that a source population is one in which births exceed deaths and emigration exceeds immigration. In sink populations, deaths exceed births and immigration exceeds emigration. Animals move from source to sink habitats either because of density-dependent competition or density-independent dispersal (Holt 1993). Delibes et al. (2001) proposed that habitat selection is a key factor underlying source-sink dynamics. When individuals avoid sink habitats, the sink does not depress the source population. However, when animals choose habitats in a maladaptive way (either because they cannot distinguish sink from source or because they prefer the sink), the overall population can decline and may go extinct.

It is well documented that human caused mortality represents the single greatest cause of death in grizzly bears, excluding dependent young, and human developments contribute to this mortality (McLellan et al. 1999, Haroldson et al. 2006, Schwartz et al. 2010). Grizzly bears are attracted to human developments in search of food. Unsecured garbage, pet food, bird feeders, livestock and livestock feed are attractants typically identified as the cause of bear-human conflicts associated with developments (Gunther et al. 2004). As suggested by Schlaepfer et al. (2002), these areas represent evolutionary traps because the sudden anthropogenic change in the environment results in attracting bears to perceived food source, but the results are maladaptive because of the increased risk of mortality.

This source-sink dynamic is consistent with findings on extinction rates and reserve sizes for large carnivores (Woodroffe & Ginsberg 1998). Areas outside reserves (areas afforded high levels of protection that represent source habitat) typically represent population sinks because large carnivores are killed by humans and most deaths occur beyond reserve boundaries. Where reserves are large relative to home ranges, many individuals can live entirely within source habitat where they are buffered from human-caused mortality sources. When source areas are small relative to home ranges, animals cannot live entirely within the reserve boundary and must use habitats that are less secure outside of reserves, which can result in reduction or even extinction of the population. This is particularly true where human killing represents the greatest threat to demographic stability. When this occurs, the survival of individuals, and ultimately of the population, is determined by the ratio of source to sink habitat within individual home ranges, the relative amount of time individuals spend in each and their cumulative effect on survival. The critical element of this dynamic is to ensure that on average recruitment equals or exceeds mortality for the population as a whole, recognizing that high human-caused mortality beyond secure habitats is expected and may exceed recruitment in some years. Maintaining a balance between recruitment and mortality is the crux of large carnivore conservation, generally (Woodroffe & Ginsberg 1998), and grizzly bear management in the GYE, specifically. Conservation and management then become a balancing act directed at minimizing or at least managing mortality for the population, recognizing that the majority of deaths for independent-aged bears will occur in sink areas. This dynamic has significant ramifications for future management of the GYE grizzly bears and how the long-term conversion of source to sink habitat associated with exurban development can potentially impact survival of the species.

We agree with the recommendations of Gude et al. (2007) that county-wide zoning and other policies that prevent or minimize subdividing large undeveloped tracts of private land in and adjacent to occupied grizzly bear habitats are likely to be critically important in preserving biodiversity and maintaining security for grizzly bears. Impacts on wildlife can be reduced if counties discourage subdividing undeveloped lands and focus future development footprints within existing town sites and adjacent subdivisions. Infill that does not increase residential development beyond the existing footprint does not add to the conversion of source habitat to sinks. However, given our finding that extremely low densities of residential development create sink habitats, tools in addition to zoning and subdivision regulation may prove more practical. The most effective means of retaining large areas of undeveloped land and conserving grizzly bear source habitat will likely require a landscape-scale approach. We suggest that local governments, wildlife management agencies and land conservation organizations focus their efforts on voluntary or voter-approved land conservation tools (e.g. land purchases, land trades, easements and open space bonds), and that they work with the owners of large, privately held tracts of suitable habitat to maintain these areas in an undeveloped condition.

Also, because grizzly bears are attracted to human developments (evolutionary traps) in search of anthropogenic foods, we suggest that communities and counties consider enacting ordinances addressing garbage and attractant management. A good example is one recently enacted in 2008 in Teton County, Wyoming. This 'bear conflict mitigation and prevention regulation' requires all residents and businesses within identified high conflict priority areas to store garbage and bird foods so they are unavailable to bears (Teaschner & Boyce 2010). A similar ordinance was adopted in 2010 by the city of Missoula, Montana, USA, which specifies provisions for the accumulation and storage of garbage within identified black bear *Ursus americanus* zones (Missoula Municipal Code 2010).

Finally, we encourage implementation of 'bear wise community programmes' on an ecosystem-wide basis by government and nongovernment organizations. The Wyoming Game and Fish Department instituted such a program in 2005, in an effort to minimize human-bear conflicts, minimize management-related bear mortalities associated with preventable conflicts and to safeguard human communities (Teaschner & Boyce 2010). Such strategies aim to achieve reduction in accessible and unnatural attractants in developed areas, public education about safe and compatible ways to live in bear country, and more widespread use of bear-resistant waste management to help minimize bear-human conflicts.

The negative environmental consequences of rural land development, including landscape fragmentation, have been widespread and extensive in USA (Gonzalez-Abraham et al. 2007, Prato 2009). Over 90% of the land in the Lower 48 states has been logged, plowed, mined, overgrazed, paved or otherwise modified from pre-settlement conditions (Terborgh & Soule 1999). Communities and counties that choose to conserve open space, adopt garbage management ordinances and institute bear wise programmes, especially at the landscape scale, can significantly reduce the negative impacts of urban and exurban sprawl on wildlife habitat in general and on secure grizzly bear habitat, in particular. Communities choosing to continue poor garbage management practices, while exerting little effort to reduce the amount of undeveloped land being consumed and converted to exurban housing can anticipate a chronic decline in suitable wildlife habitat and bear habitat and an increase in bear-human conflicts. With good planning, the West should be able to accommodate additional growth yet retain the open space and abundant wildlife populations that attract people in the first place.

Acknowledgements - we thank K. Barber for providing GIS layers beyond the recovery zone. We thank K.K. West and J.L. Kershner for constructive reviews of earlier drafts. We appreciate efforts of J. Hilty and C. Servheen who served as preliminary reviewers of the draft manuscript as part of the U.S.G.S. Fundamental Sciences Practices requirement. Our study was funded by the U.S. Geological Survey, Northern Rocky Mountain Science Center. Our study complied with current laws of the United States of America, was conducted in accordance with animal care and use guidelines, and was approved by the United States Geological Survey Institutional Animal Care and Use Committee. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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