Animal Conservation (2004) **7**, 1–7 © 2004 The Zoological Society of London. Printed in the United Kingdom DOI:10.1017/S1367943003001203

Carnivore re-colonisation: reality, possibility and a non-equilibrium century for grizzly bears in the Southern Yellowstone Ecosystem

Sanjay Pyare[1]*, Steve Cain[2], Dave Moody[3], Chuck Schwartz[4] and Joel Berger[5]

[1] Denver Zoological Foundation, 1650 Hole in the Wall Rd, Potomac MT 59823, USA
[2] Office of Science and Resource Management, Grand Teton National Park, Box 170, Moose, Wyoming 83012, USA
[3] Wyoming Game and Fish, Lander, Wyoming, 82520, USA
[4] USGS Northern Rocky Mountains Service Center, Montana State University, Bozeman, Montana 59717, USA
[5] North American Program, Wildlife Conservation Society, Box 340, Moose, Wyoming 83012, USA

(Received 21 October 2002; accepted 6 August 2003)

Abstract

Most large native carnivores have experienced range contractions due to conflicts with humans, although neither rates of spatial collapse nor expansion have been well characterised. In North America, the grizzly bear (*Ursus arctos*) once ranged from Mexico northward to Alaska, however its range in the continental USA has been reduced by 95–98%. Under the U. S. Endangered Species Act, the Yellowstone grizzly bear population has re-colonised habitats outside Yellowstone National Park. We analysed historical and current records, including data on radio-collared bears, (i) to evaluate changes in grizzly bear distribution in the southern Greater Yellowstone Ecosystem (GYE) over a 100-year period, (ii) to utilise historical rates of re-colonisation to project future expansion trends and (iii) to evaluate the reality of future expansion based on human limitations and land use. Analysis of distribution in 20-year increments reflects range reduction from south to north (1900–1940) and expansion to the south (1940–2000). Expansion was exponential and the area occupied by grizzly bears doubled approximately every 20 years. A complementary analysis of bear occurrence in Grand Teton National Park also suggests an unprecedented period of rapid expansion during the last 20–30 years. The grizzly bear population currently has re-occupied about 50% of the southern GYE. Based on assumptions of continued protection and ecological stasis, our model suggests total occupancy in 25 years. Alternatively, extrapolation of linear expansion rates from the period prior to protection suggests total occupancy could take > 100 years. Analyses of historical trends can be useful as a restoration tool because they enable a framework and timeline to be constructed to pre-emptively address the social challenges affecting future carnivore recovery.

INTRODUCTION

Globally, large and medium-sized carnivores have experienced dramatic range reductions (Gittleman & Gomper, 2001). These include extinctions for the lion (*Panthera leo*) and tiger (*P. tigris*) in Pakistan and Iran, for the cheetah (*Acinocynx jubatus*) in India, the wild dog (*Lycaon pictus*) in at least 25 subsaharan African countries and for wolves (*Canis lupus*) from Great Britain and Mexico (Creel & Creel, 1996; Woodroffe, 2001). This pattern of regional collapse also characterises the grizzly bear (*Ursus arctos*) in North America and Europe. However, the grizzly bear has also experienced local range expansions. In Fennoscandia, western Russia, Ukraine and Slovenia, following several centuries of human persecution, protective measures initiated in the latter half of the 20th century have enabled colonisation of vacant range (Chestin *et al.*, 1992; Swenson *et al.*, 1995; Adamic, 1996; Swenson, Sandegren & Soderberg, 1998*a*; Swenson *et al.*, 1998*b*). Although such instances illustrate recovery at a local ecological scale, long-term, geographical expansion has received less attention (but see Mattson, Blanchard & Knight, 1992; Breitenmoser *et al.*, 2001; Frank & Woodroffe, 2001). An assessment of the difference between biological possibility and the reality of expansion is necessary to focus attention on future carnivore conservation efforts (Linnell *et al.*, 2001; MacDonald, 2001).

The grizzly bear occupied substantial portions of western North America as late as the mid-19th century, but by 1970 it was reduced to 2% of its former range in the lower 48 states of the USA (U.S. Fish and Wildlife Service, 1982; Mattson & Merrill, 2002). By 1975, when grizzly bears were federally protected in the USA, five remnant populations remained outside Alaska. Two have since expanded – the Yellowstone and the Northern Continental Divide populations, both of which were previously restricted to national parks (Bader, 2000). In the Yellowstone ecosystem, for example, the

*All correspondence to: S. Pyare. Tel: 406 244 0982.
E-mail: sanjay_pyare@hotmail.com

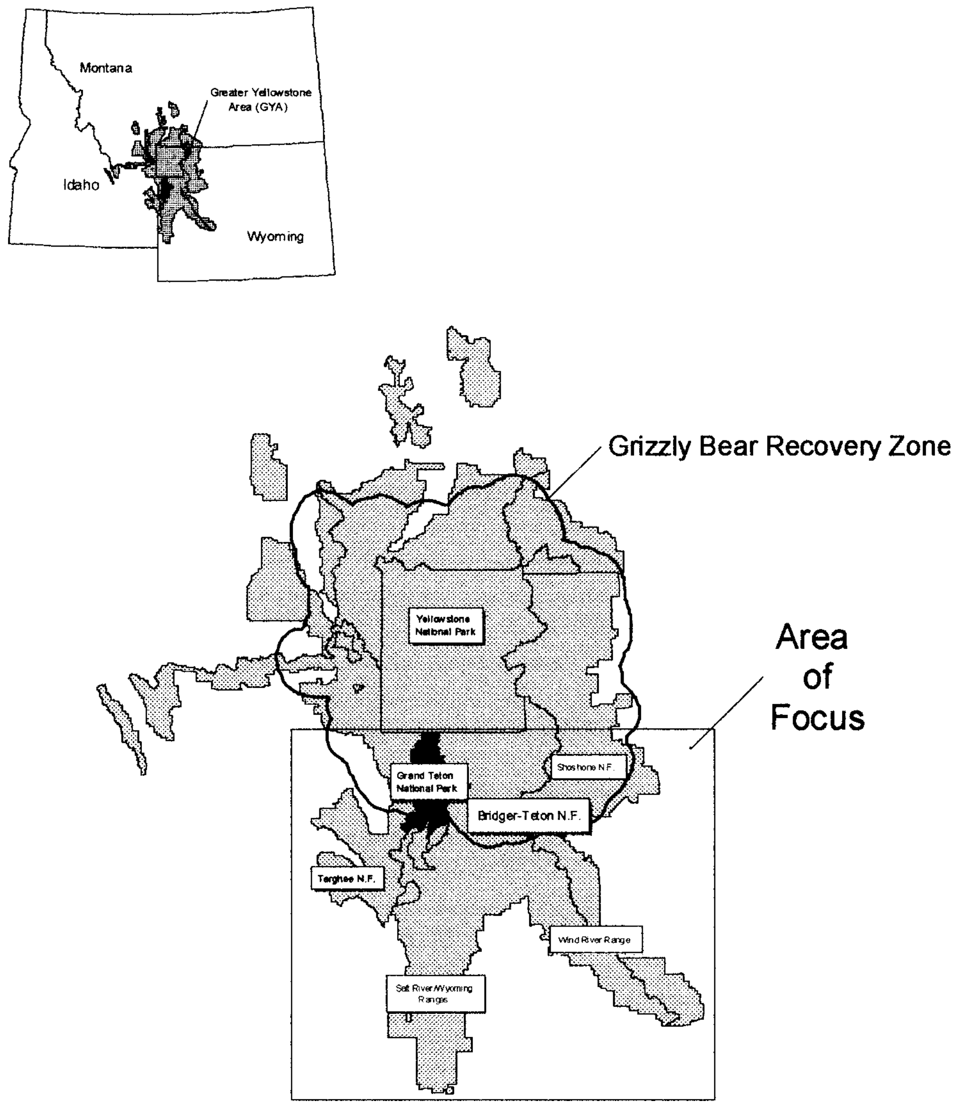

Fig. 1. Map showing the 24 000 km^2 study area within the Greater Yellowstone ecosystem and the federal grizzly bear recovery zone (with its 10-mile buffer).

grizzly bear population currently occupies areas beyond the Yellowstone federal recovery zone (Schwartz, 2001; Schwartz *et al.*, 2002), although the extent of population recovery is unclear (Eberhardt, Blanchard & Knight, 1994; Boyce, 1995; Pease & Mattson, 1999). The population has been well studied in more northern portions of the recovery zone, including Yellowstone National Park (Craighead, Sumner & Mitchell, 1995; Schwartz *et al.*, 2002). However, the status of grizzly bears in the extensive region to the south of Yellowstone National Park has been less thoroughly investigated.

Our goals were as follows: (i) to analyse the 100-year history of grizzly bear distribution in the southern Greater Yellowstone Ecosystem (GYE); (ii) to predict future expansion possibilities and (iii) to illustrate how analyses of spatial collapse and subsequent expansion can help frame future conservation options. Our efforts have particular relevance for future recovery planning by state agencies, which will soon decide where this population will be allowed to occur once removed from federal protection under the U. S. Endangered Species Act.

MATERIALS AND METHODS

The GYE is a 57 000 km^2 region in the Rocky Mountains that contains portions of three states, Wyoming, Montana and Idaho, and includes two national parks (Fig. 1). Although about 500 000 people live on its perimeter and about four million people visit the parks annually, > 73% of this ecosystem currently exists in a secure, roadless condition (Bader, 2000). A rugged and mountainous landscape, in conjunction with the secretive nature of the grizzly bear, has precluded precise estimates of population density (Eberhardt *et al.*, 1994; Mattson & Craighead, 1994; Boyce, 1995; Mattson, 1997*a*; Pease & Mattson, 1999).

In this paper, the spatial analysis will be restricted to areas south of the boundary between Yellowstone and

Table 1. Organization of grizzly bear distribution map and period-specific data sources utilized to approximate distribution boundaries

Date	Period depicted	Data source(s)	Data type(s)
1900	Before 1900	Merriam (1922)	Reports
		USFWS (1982)	Reports
1920	By 1920	Merriam (1922)	Reports
1940	By 1940	Murie (1948)	Livestock conflicts, interviews
1960	By 1960	Murie (1948)	Livestock conflicts, interviews
		Negus & Findley (1959)	Museum specimens, reports
		Craighead *et al.* (1988)	Mortalities
1980	1961–1980	IGBST, unpublished data	Distribution of females with cubs, home-ranges, mortalities, verified observations
		Basile (1982)	Observations
		Hoak, Clark & Weaver (1979); Hoak, Clark & Wood (1981)	Reports, interviews
		Craighead *et al.* (1988)	Mortalities
		Blanchard, Knight & Mattson (1992)	Reports, telemetry locations
		NPS, unpublished data	Verified sightings
2000	1981–2000	IGBST, unpublished data	Home-ranges, mortalities, verified observations
		NPS, unpublished data	Verified observations

IGBST, Interagency Grizzly Bear Study Team; NPS, National Parks Service.

Grand Teton National parks (Fig. 1) because the history and population trends of grizzly bears have been well documented in the northern portions of the ecosystem (Craighead *et al.*, 1995; Bader, 2000; Schwartz *et al.*, 2002).

We focused on a 24 000 km^2 mosaic of mostly public land that is managed by various federal and state agencies. Our analysis of changes in grizzly bear distribution during 1900–2000 was divided into 20-year periods. For each, we used various data sources for grizzly bear occurrence (Table 1) to create digital maps of bear distribution using ArcView GIS 3.2 (ESRI, Redlands, CA). We digitised reports, interviews, conflicts, mortalities and observations as points. We created a polygon for the 1920 source data, a hand-drawn distribution map by Merriam (1922). For the 1980 and 2000 source data, we created a composite polygon from the following layers: composite distribution of females with cubs, composite home ranges for radio-collared bears (all ages and both genders) and a composite layer of conflict and mortality occurrences. For maps with multiple data sources, point locations and polygons were merged to create a single coverage for each 20-year period. Because outlying point locations could unrealistically influence our distribution maps and we were striving to depict where grizzly distribution was relatively continuous, we eliminated point locations that were > 30 km from other locations. Given typical dispersal distances of 27 km (Blanchard & Knight, 1991; Woodroffe, 2001) we felt this distance was reasonable. This procedure resulted in the dismissal of no more than three points for any period. To create a final distribution polygon for each period, we manually digitised an outer boundary that included 100% of all remaining points.

To describe rates of range expansion during the period 1940–2000, we fitted exponential functions to simple plots of area occupied (km^2) against time (year). We also used this exponential function, as well as simple linear functions fitted to expansion rates during two 20-year time periods (namely 1960–1980 and 1980–2000), to derive estimates of the time hypothetically required to achieve 'total occupancy' of the southern GYE. We defined total occupancy as a condition in which grizzly bear occurrence is continuously distributed throughout the available habitat and made no assumptions about population densities or carrying capacities.

We attempted to determine whether rates of geographical expansion were associated with deterministic annual growth rates, an effort that was designed to check for a possible correlation with changes in grizzly bear distribution. In this exercise, we used 20-year changes in the occupied range of bears and evaluated them against a series of deterministic annual (λ) growth rates for the 60-year period of range expansion. We varied λ by intervals of 0.01 over a spectrum of values from 0.01 to 0.10. For each λ, a separate analysis was performed to derive projected population size, which, in all simulations, began at 50 individuals in 1940 and was repeated annually for each of the 60 years until the year 2000. Linear correlation was subsequently used to assess the amount of variance in growth rates that was explained by spatial coverage.

RESULTS

By 1920, the grizzly bear population persisted only in the more remote and mountainous regions of the southern GYE –, in what was to become the Bridger–Teton Wilderness Area, in the Teton Range and in isolated mountain ranges farther south (i.e. the Salt River/Wyoming Ranges and the Wind River Range: Fig. 2). Anecdotal records from the 1920s and 1930s indicate that

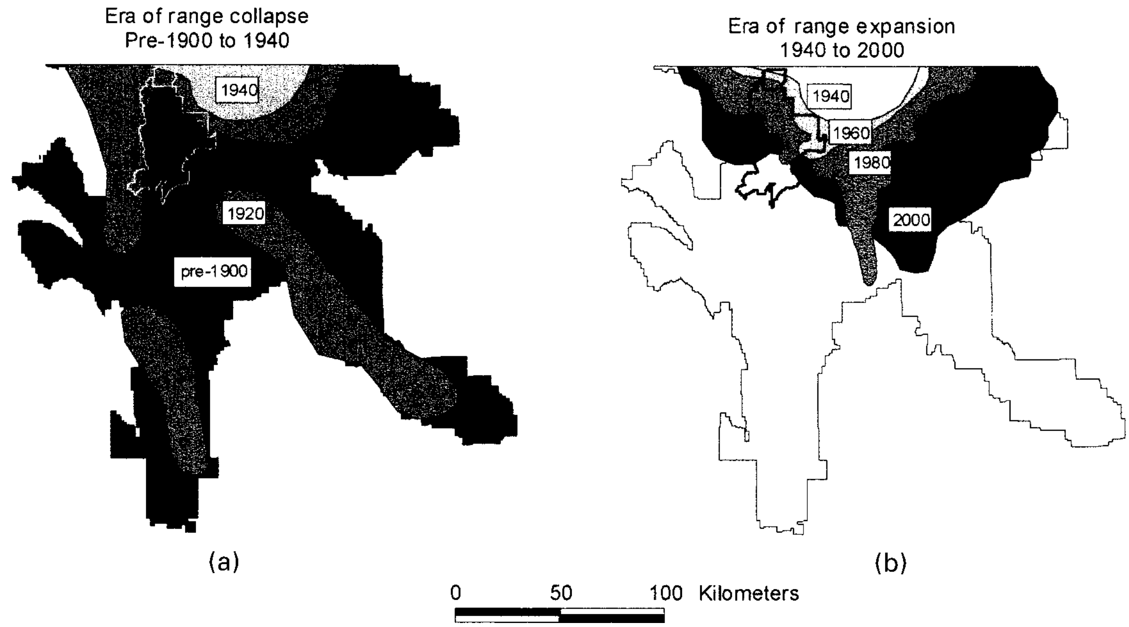

Fig. 2. Depiction of grizzly bear distribution in the southern Yellowstone ecosystem during two distinct periods. (a) During an era of range collapse prior to 1940, grizzly bears declined in all except the northern portions of the study area, persisting only near the boundary of Grand Teton National Park (boundary shown) and Yellowstone National Park, and in adjacent Teton Wilderness Area. (b) After this period, grizzly bears appeared progressively further south, although they are essentially absent from half of their original range.

concerted efforts to decimate bears were common and isolated populations in the southern reaches of the ecosystem had probably been eliminated. By 1940, the grizzly bear was rare, and it was nearly eliminated from the entire southern GYE, continuing to persist only in areas near Yellowstone National Park and adjacent roadless areas, i.e. what is now the Bridger–Teton Wilderness Area. It was also absent from Grand Teton National Park at this time. By 1960, however, the population had expanded to the eastern periphery of Grand Teton National Park. Evidence for expansion was limited elsewhere. During the next 20 years, the grizzly was legally protected. It returned to northeastern portions of Grand Teton National Park and extended its range almost 60 km southward.

Between 1980 and 2000, the population returned to nearly half of its former range in the southern GYE. Expansion was particularly evident in the southern and eastern portions of the ecosystem, including the northern Wind River Range and Shoshone National Forest, but was less apparent in western and southwestern portions of the ecosystem. Reports of grizzly bears in Grand Teton National Park increased rapidly between the late 1970s and mid-1990s; more so than the proportional increase in a visitor-use index during the same period. This suggests the increase was real and not merely a consequence of greater reporting rates by personnel or visitors (Fig. 3).

The geographical spread of the grizzly population fitted an exponential function, doubling roughly every 20 years from 1940 to 2000 (Fig. 4). The change in area occupied during 1980–2000 equaled the total area occupied during the previous 40 years. Simple extrapolation of the trend observed from 1940–2000 suggests total occupancy could theoretically occur in 25 years (Fig. 5). Alternatively, if the expansion pattern remains similar to that observed during the last 20 years only (i.e. 1980–2000), or resembles the even slower pattern observed during the previous 20-year period (1960–1980, prior to protection), total occupancy would occur in either 48 or 103 years, respectively.

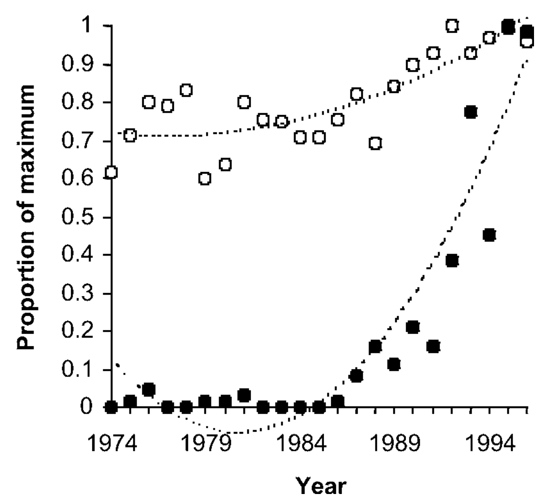

Fig. 3. Graph showing the relative trends in visitor use during a period of increased grizzly bear reports in Grand Teton National Park, 1974–1996. Visitor use data were derived from nearby Yellowstone National Park due to greater consistency in methods of data collection. Not shown are data for the 5-year periods during which grizzly bears had been first reported and, consequently the likelihood of reporting may have been over-biased (1969–1973) and the period during which knowledge of bears became relatively commonplace and thus, reporting became less likely (1997–2001). -○-, number visitors; -●-, number of bear reports.

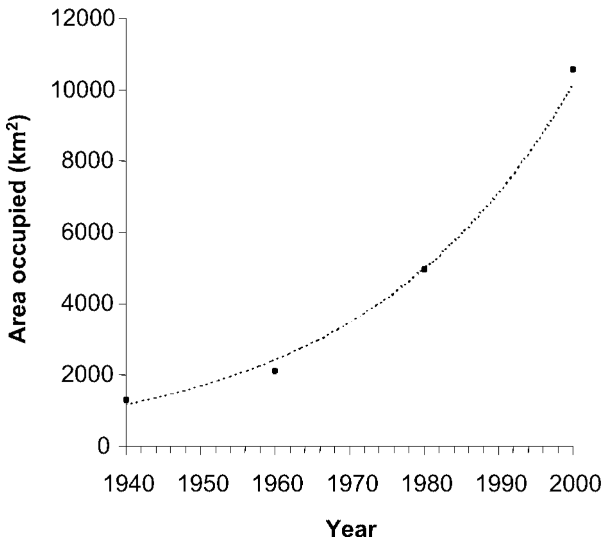

Fig. 4. Graph of the estimates of the area that grizzly bears occupied in the southern Yellowstone ecosystem during a period of range expansion (1940–2000). The rate of expansion during this period increased exponentially ($R^2 = 0.96$).

We evaluated whether the spatial pattern of population expansion was associated with deterministic population growth by plotting changes in population size, repeated for different λ, against range coverage. The amount of variance in range coverage explained by λ at 0.01 intervals from 0.01 to 0.10 was either 0 or < 0.01; an overall indication of the lack of any relationship between these two variables.

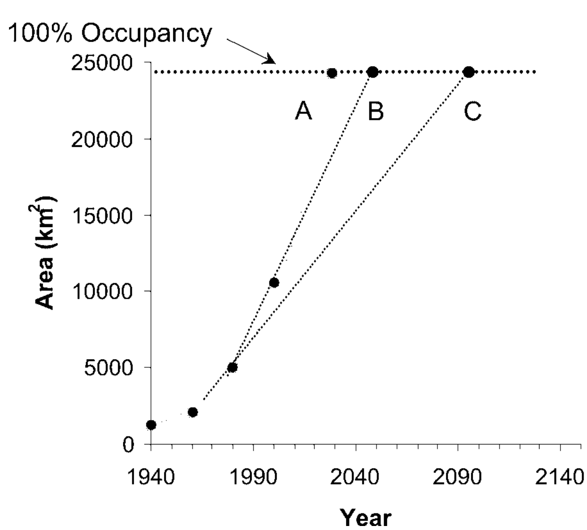

Fig. 5. Graph of the estimates of time that is theoretically required for total occupancy by grizzly bears in the southern GYE. Total occupancy is defined as a condition in which grizzly bear occurrence is continuously distributed throughout the available habitat. Estimates were derived from assumptions of (A) continuance of the exponential expansion rates observed during 1940–2000 and continuance of the linear expansion patterns from (B) 1980–2000 and (C) 1960–1980.

DISCUSSION

Protection and the inevitability of expansion

Despite its obvious simplicity, our analysis characterises the regional history of the grizzly bear population in the southern GYE. Firstly, the population has substantially expanded its distribution to areas previously vacant for 60–80 years. Secondly, expansion was most evident in the southern and eastern portions of our study area. Thirdly, the rate of expansion was greatest during the last 20 years. Range expansion has occurred in a population that has been growing (Eberhardt *et al.*, 1994; Boyce, 1995; Pease & Mattson, 1999).

Methodologically, our approach was limited by map accuracy. We used a simple procedure to delineate the outer distribution boundary for each period. Furthermore, our findings were sometimes based on qualitative historical data. For instance, our depiction of the 1920 distribution was derived from a hand-drawn map (Merriam, 1922). Greater map accuracy, however, was unlikely to have yielded a different overall picture of range expansion. For instance, had we underestimated the area occupied by bears in 1940 and 1960 by 10%, a possible scenario given that grizzly bears were not intensively monitored during these periods, the estimate of time required for total occupancy would have changed by only + 1.7 years. In addition, our analysis relating range expansion to population growth rate was based on deterministic population growth that spanned the entire study period. This assumption of constant growth may be an inaccurate descriptor of growth rates in grizzly bear populations (Eberhardt *et al.*, 1994; Pease & Mattson 1999).

Our historical analysis provides a framework and timeline for the consideration of future expansion: total occupancy of the ecosystem could occur in a few decades. Our estimate of 25 years for this to occur, however, is only a theoretical upper limit. It is dependent on exponential grizzly bear expansion throughout the re-colonisation process. Obviously, this projection is heuristic, since it involves an assumption that several factors will remain unchanged, including (i) biological processes affecting population expansion (e.g. vagility, dispersal rates and distances, fecundity), (ii) food availability, (iii) environmental stasis, (iv) connectivity among colonisation areas and (v) human encounter rates. Our other estimates of 48 or 104 years for colonisation to occur may, however, be more realistic because they are extrapolated from simple linear expansion rates measured for the last two 20-year periods.

Rates of grizzly expansion and humans

The detrimental effects of human activities on grizzly bears are well established (Knight, Blanchard & Eberhardt, 1988; Mattson *et al.*, 1992; Mattson, Knight & Blanchard, 1994; Mattson, 1995; Weaver, Paquet & Ruggiero, 1996; Woodroffe, 2000; Clark *et al.*, 2001). Thus, in evaluating which time-frame is most realistic, and indeed whether full occupancy of the southern GYE is possible, we suspect that grizzly expansion will continue to be most affected by factors that are almost entirely in the human domain: fragmentation of landscapes by human development and rates of lethal contact with humans (factors iv and v, above). The likelihood that other factors will limit expansion is possible, but these may be mitigated through the occupancy of different habitats by bears (Mattson & Merrill, 2002) and by the generalist nature of bear foraging (Mattson *et al.*, 1992; Green, Mattson & Peek, 1997; Mattson, 1997*b*; Hildebrandt *et al.*, 1999; Jacoby *et al.*, 1999). The possibility that expansion patterns change when humans interact with these other factors should not be discounted (Schwartz, 2001), as illustrated by the increase in mortality levels around human settlements during declines in the seed crops of white bark pine (*Pinus albicaulis*), during the ungulate hunting seasons (Mattson *et al.*, 1992), or when bear movements are altered due to wildfire (Blanchard & Knight, 1990).

In the Wind River and Wyoming Ranges (Fig. 1), opportunities for continuing re-colonisation are greatest even when considered within the context of human settlements and land use. Although bears were essentially extinct here 60–80 years ago, human population densities are still among the lowest in the GYE. For the entire 12 500 km^2 of Sublette County, Wyoming, an area in which essentially contiguous habitat remains, human density is 0.46 persons/km^2 compared to 1.97 persons/km^2 for the entire state of Wyoming (U.S. Census Bureau, 2000). Thus, except for the grazing of domestic livestock, conflicts with humans should remain low. However, our assumption of stasis among several factors affecting expansion rates may not be realistic. Firstly, the predicted effects of global warming may diminish white bark pine seed production (Mattson & Reid, 1991), resulting in an increase in the use of lower elevation habitats by bears, consequently bringing bears into closer contact with human settlements. Secondly, despite the protected status of grizzly bears, human population growth and land impacts will continue to increase. Thus, while it is possible to predict rates of geographical expansion, the more daunting challenge is making realistic predictions involving the effects of human behaviour and land use.

The progress of grizzly bear recovery in the Yellowstone ecosystem is an important conservation case study (Pyare & Berger 2003) and, clearly, our historical analysis of grizzly bear distribution highlights a success among conservation efforts (Schwartz *et al.*, 2002). In addition, our simple model illustrates that, in as few as 25 years, the Yellowstone grizzly bear population could re-occupy large areas south of the Yellowstone recovery zone, such as the Wind River and Wyoming Ranges. This suggests that there is only a limited time-frame in which to identify and address the social and practical challenges surrounding grizzly occurrence in potential expansion zones. Establishing a timeline for expansion has important implications for future Yellowstone grizzly bear recovery efforts. Firstly, a better understanding of the possible rates at which grizzly bears could expand allows agencies to pre-emptively plan and develop realistic policies pertaining to the management of grizzly bear occurrence in the future. This has particular relevance for state agencies that are currently establishing and implementing plans for grizzly bear management and, following federal de-listing, will have a more direct influence on grizzly distribution in the future. Secondly, in the event that expansion rates continue and grizzly bear presence is tolerated outside the recovery zones following federal de-listing, recognition of the possible rates at which bears can expand also allows groups to plan for and pre-emptively mitigate conflicts that might occur between humans and bears in potential expansion zones. Thus, timelines to achieve conservation benchmarks, such as those provided here, allow agencies and the conservation community at-large to more effectively gauge and allocate the resources required to minimise conflict and maintain conservation successes such as the grizzly bear.

Acknowledgements

The National Science Foundation, the Wildlife Conservation Society, Charles Englehard Foundation, Jackson Hole Foundation, the University of Nevada, Reno and Denver Zoological Foundation supported S.P. and J.B. during the drafting of this manuscript. The U.S. Interagency Grizzly Bear Study Team, which included the U.S. Geological Survey, Northern Rocky Mountain Science Center, Wyoming Game and Fish Department, Yellowstone National Park, U.S. Fish and Wildlife Service, Montana Department of Fish, Wildlife and Parks, Grand Teton National Park, Idaho Fish and Game Department and the U.S. Forest Service, helped facilitate this research and provided funding for the data used to determine bear distribution during the 1970-1990s. We especially thank D. Knight and B. Blanchard, retired members of IGBST, who shepherded the study team from its inception in 1973 through to 1997. For help with data collection and/or bear capture efforts, we thank M. Haroldson, S. Podruzny, J. Jonkel, K. Gunther, K. Inberg, B. Schleyer, C. Dickinson, M. Lamoreux, M. Ternent, M. Biel, and G. Holm. We also thank pilots D. Stradley, R. Stradley, S. Monger, G. Lust, and R. Hyatt, who have flown grizzly bear radio-tracking flights in the GYE for many years. For providing technical assistance and helpful comments about this manuscript, we thank R. Jachowski, J. Ray, T. Foxx, D. Hammond, W. Koelfgen, K. McCoy, K. White and S. Wolff. GIS analysis was made possible through software provided by Environmental Research Systems, Inc. (ESRI).

REFERENCES

Adamic, M. (1996). An expanding brown bear population in Slovenia: current management problems. *J. Wildl. Res.* **1**: 297–300.

Bader, M. (2000). Distribution of grizzly bears in the U.S. northern Rockies. *Northwest Sci.* **74**: 325–333.

Basile, J. V. (1982). *Grizzly bear distribution in the Yellowstone area, 1973–1979.* U.S.D.A. Forest Service Research. Note INT-321. Ogden, UH: U.S. Forest Service.

Blanchard, B. M. & Knight, R. R. (1990). Reactions of grizzly bears to wildfire in Yellowstone National Park, Wyoming. *Can. Field. Nat.* **104**: 592–594.

Blanchard, B. M. & Knight, R. R. (1991). Movement of Yellowstone grizzly bears. *Biol. Conserv.* **58**: 41–67.

Blanchard, B. M., Knight, R. R. & Mattson, D. J. (1992). Distribution of Yellowstone grizzly bears during the 1980s. *Am. Midl. Nat.* **128**: 332–338.

Boyce, M. (1995). *Population viability analysis for grizzly bears: a critical review.* A report to the Interagency Grizzly Bear Committee. unpublished.

Breitenmoser, U., Breitenmoser-Wursten, C., Carbyn, L. & Funk, S. M. (2001). Assessment of carnivore reintroductions. In *Carnivore conservation*: 241–282. Gittleman, J. L., Funk, S. M., McDonald, D. & Wayne, R. K. (Eds). Cambridge: Cambridge University Press.

Chestin, I. E., Gubar, Y. P., Sokolov, V. E. & Lobachev, V. S. (1992). The brown bear in the U.S.S.R: numbers, hunting, systematics. *Ann. Zool. Fenn*. **29**: 57–68.

Clark, T. W., Mattson, D. J., Reading, R. P. & Miller, B. J. (2001). Interdisciplinary problem solving in carnivore conservation: an introduction. In *Carnivore conservation*: 223–240. Gittleman, J. L., Funk, S. M., McDonald, D. & Wayne, R. K. (Eds). Cambridge: Cambridge University Press.

Craighead, J. J., Greer, K. R., Knight, R. R. & Pac, H. I. (1988). *Grizzly bear mortalities in the Yellowstone ecosystem 1959–1987.* Report. Bozeman, MA: Craighead Wildlife-Wildlands Institute.

Craighead, J. J., Sumner, J. S. & Mitchell, J. A. (1995). *The grizzly bears of Yellowstone.* Washington DC: Island Press.

Creel, S. & Creel, N. (1996). Limitation of African wild dogs by competition with larger carnivores. *Conserv. Biol*. **10**: 526–538.

Eberhardt, L. L., Blanchard, B. M. & Knight, R. R. (1994). Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Can. J. Zool.* **72**: 360–363.

Frank, L. G. & Woodroffe, R. (2001). Behaviour of carnivores in exploited and controlled populations. In *Carnivore conservation*: 419–442. Gittleman, J. L., Funk, S. M., McDonald, D. & Wayne, R. K. (Eds). Cambridge: Cambridge University Press.

Gittleman, J. L. & Gomper, M. E. (2001). The risk of extinction – what you don't know will hurt you. *Science* **291**: 997–999.

Green, G. I., Mattson, D. J. & Peek, J. M. (1997). Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *J. Wildl. Mgmt.* **61**: 1040–1055.

Hildebrandt, G. V., Schwartz, C. C., Robins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M. & Servheen, C. (1999). The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can. J. Zool.* **77**: 132–138.

Hoak, J. H., Clark, T. W. & Weaver, J. L. (1979). Of grizzly bears and commercial outfitters in Bridger-Teton National Forest. *Int. Conf. Bear. Res. Mgmt.* **5**: 110–117.

Hoak, J. H., Clark, T. W. & Wood, B. (1981). Grizzly distribution, Grand Teton National Park area, Wyoming. *Northwest Sci*. **55**: 245–247.

Jacoby, M. E., Hildebrand, G. V., Servheen, C., Schwartz, C. C., Arthur, S. M., Hanley, T. A., Robbins, C. T. & Michener, R. (1999). Trophic relations of brown and black bears in several western North American ecosystems. *J. Wildl. Mgmt.* **63**: 921–929.

Linnell, J. C. D., Swenson, J. E. & Anderson, R. (2001). Predators and people: conservation of large carnivores is possible at high human densities if management policy is favorable. *Anim. Conserv*. **4**: 345–349.

Knight, R. R., Blanchard, B. & Eberhardt, L. L. (1988). Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. *Wildl. Soc. Bull*. **16**: 121–125.

MacDonald, D. W. (2001). Postscript – carnivore conservation: science, compromise and tough choices. In *Carnivore conservation*: 524–538. Gittleman, J. L., Funk, S. M., McDonald, D., & Wayne, R. K. (Eds), Cambridge: Cambridge University Press.

Mattson, D. J., Knight, R. R. & Blanchard, B. M. (1994). The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Int. Conf. Bear. Res. Mgmt.* **7**: 259–273.

Mattson, D. J. (1995). Human impacts on bear habitat use. *Int. Conf. Bear. Res. Mgmt*. **8**: 33–56.

Mattson, D. J. (1997*a*). Sustainable grizzly bear mortality calculated from counts of females with cubs of the year: an evaluation. *Biol. Conserv*. **81**: 161–177.

Mattson, D. J. (1997*b*). Use of ungulates by Yellowstone grizzly bears. *Biol. Conserv*. **81**: 161–177.

Mattson, D. J., Blanchard, B. & Knight, R. R. (1992). Yellowstone grizzly bear mortality, human habituation, and white bark pine seed crops. *J. Wildl. Mgmt*. **56**: 432–442.

Mattson, D. J. & Craighead, J. J. (1994). The Yellowstone grizzly bear recovery program: uncertain information, uncertain policy. In *Endangered Species Recovery*: 101–129. Clark, T. W., Reading, R. P. & Clark, A. L. (Eds). Washington, DC: Island Press.

Mattson, D. J. & Merrill, T. (2002). Extirpations of grizzly bears in the western contiguous United States. *Conserv. Biol*. **16**: 1123–1136.

Mattson, D. J. & Reid, M. M. (1991). Conservation of the Yellowstone grizzly bear. *Conserv. Biol.* **5**: 364–372.

Merriam, C. H. (1922). Distribution of grizzly bears in U.S. *Outdoor Life* **L**: 405–406.

Murie, A. (1948). Cattle on grizzly bear range. *J. Wildl. Mgmt.* **56**: 57–68.

Negus, N. C. & Findley, J. S. (1959). Mammals of Jackson Hole, Wyoming. *J. Mammal*. **40**: 371–381.

Pease, C. M. & Mattson, D. J. (1999). Demography of the Yellowstone grizzly bears. *Ecology* **80**: 957–975.

Pyare, S. & Berger, J. (2003). Beyond demography and de-listing: ecological recovery for Yellowstone's grizzly bears and wolves. *Biol. Conserv.* **113**: 63–72.

Schwartz, C. C. (2001). The paradigm of grizzly bear restoration in North America. In *Large mammal restoration*: 225–229. Maehr, D. S., Noss, R. F. & Larkin, J. L. (Eds). Covello: Island Press.

Schwartz, C. C., Haroldson, M. A., Gunther, K. A. & Moody, D. (2002). Current distribution of grizzly bears in the Greater Yellowstone ecosystem, 1990–2000. *Ursus* **13**: 203–213.

Swenson, J. E., Wabakken, P., Sandegren, F., Bjarvall, A., Franzen, R. & Soderberg, A. (1995). The near extinction and recovery of brown bears in Scandanavia in relation to the bear management policies of Norway and Sweden. *Wildl. Biol*. **1**: 11–25.

Swenson, J. E., Sandegren, F. & Soderberg, A. (1998*a*). Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *J. Anim. Ecol.* **67**: 819–826.

Swenson, J. E., Sandegren, F., Bjarvall, A. & Wabakken, P. (1998*b*). Living with success: research needs for an expanding brown bear population. *Ursus* **10**: 17–23.

U.S. Census Bureau (2000). Data taken from the interactive queries section on: http://www.census.gov.

U.S. Fish and Wildlife Service (1982). *Grizzly bear recovery plan*. Missoula, MA: U.S. Fish and Wildlife Service.

Weaver, J. L., Paquet, P. C. & Ruggiero, L. F. (1996). Resilience and conservation of large carnivores. *Conserv. Biol.* **10**: 964–976.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines in large carnivores. *Anim. Conserv.* **3**: 165–173.

Woodroffe, R. (2001). Strategies for carnivore conservation: lessons from contemporary extinctions. In *Carnivore conservation*: 61–92. Gittleman, J. L., Funk, S. M., McDonald, D. & Wayne, R. K. (Eds). Cambridge: Cambridge University Press.