Available online at www.sciencedirect.com
ScienceDirect
Geomorphology 79 (2006) 448–459
GEOMORPHOLOGY
www.elsevier.com/locate/geomorph

Human-induced changes in animal populations and distributions, and the subsequent effects on fluvial systems

David R. Butler *

Department of Geography, Texas State University-San Marcos, San Marcos, TX 78666-4616, USA

Received 6 February 2006; received in revised form 6 June 2006; accepted 6 June 2006
Available online 9 August 2006

Abstract

Humans have profoundly altered hydrological pathways and fluvial systems through their near-extirpation of native populations of animal species that strongly influenced hydrology and removal of surface sediment, and through the introduction of now-feral populations of animals that bring to bear a suite of different geomorphic effects on the fluvial system. In the category of effects of extirpation, examples are offered through an examination of the geomorphic effects and former spatial extent of beavers, bison, prairie dogs, and grizzly bears. Beavers entrapped hundreds of billions of cubic meters of sediment in North American stream systems prior to European contact. Individual bison wallows, that numbered in the range of 100 million wallows, each displaced up to 23 m^3 of sediment. Burrowing by prairie dogs displaced more than 5000 kg and possibly up to 67,500 kg of sediment per hectare. In the category of feral populations, the roles of feral rabbits, burros and horses, and pigs are highlighted. Much work remains to adequately quantify the geomorphic effects animals have on fluvial systems, but the influence is undeniable.

Keywords: Zoogeomorphology; Geomorphology and animal impacts; Fluvial systems; Bison and prairie dogs; Feral animals

1. Introduction

In recent years an increasing appreciation has developed for the role of native and introduced animals as geomorphic agents capable of widespread landscape change (e.g., Butler, 1995). In the case of native animals, human impacts have reduced geographic ranges and population numbers of an extensive list of geomorphically significant animals, whereas introduced animals have created widespread and often deleterious geomorphic activity in the removal of vegetation and corresponding direct and indirect erosional responses. Although several chapters in *Man's Role in Changing the Face of the Earth* (Thomas, 1956) describe human modifications of animal populations, either through removal or reduction of native populations, such as bison, or through the introduction of domesticated or feral animals, none examined the changing geomorphic landscape caused by removal of native animal species and replacement with introduced ones.

Indirect effects of human impacts on geomorphically significant animal populations occur through the alteration of habitat and by removal of predatory species. In the case of the former, human influences on the zoological aspects of aquatic systems have altered animal populations and attendant zoogeomorphic processes. For example, dam construction or removal has profound implications on accessibility to, and protection of, spawning grounds for fish. Salmonid species, such as salmon and trout, directly

---

* Tel.: +1 512 245 7977; fax: +1 512 245 8353.
E-mail address: db25@txstate.edu.

0169-555X/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.geomorph.2006.06.026

influence the geomorphology and sedimentology of stream beds through excavation of nests, or "redds" (see Butler, 1995, and references therein for a more complete description and references). Water pollution and stream eutrophication also profoundly alter native animal populations within and along riparian corridors, in turn affecting the geomorphic impacts of those animals.

In this paper, two contrasting but complementary tasks are undertaken to elucidate the geomorphic role of animals, particularly in the context of the impact on fluvial systems: (1) case studies are examined of the geomorphic effects of animals whose native ranges and numbers have been strongly, negatively impacted by human impact; and (2) several cases are illustrated where human introduction of feral species has had wide-ranging geomorphic impacts on sediment budgets and fluvial systems. *Direct geomorphic effects* on fluvial systems by damming of, and trampling and digging along, streams are examined first. *Indirect geomorphic effects* on streams are subsequently described through an examination of animal impacts on hydrologic responses of landscapes, including impacts on water and sediment loads.

Certain topics are not in this synthesis. The causal links from human impacts on streams to population changes in animals, and from there to changes in geomorphic processes and/or process intensities, are, unfortunately, little studied in the geomorphic literature. Similarly, the removal of predator animal species has allowed the expansion of prey species, with attendant potential geomorphic impacts on basin hydrology and stream systems that have been virtually undocumented in the geomorphic literature. For example, the removal of large predators and changes in habitat have led to the expansion of populations of several species of deer in parts of the United States. The white-tailed deer (*Odocoileus virginianus*) causes severe impacts on the dynamics of seedlings in riparian corridors (Seagle and Liang, 2001), and causes profound shifts in the distribution of nitrogen within forests and croplands (Seagle, 2003); but the geomorphic impacts of this expansion remain undocumented. For these reasons, neither the topic of human impact on stream habitats through activities such as damming and pollution, nor the effects of predator reduction, are pursued further in this paper while still recognizing the possible profound geomorphic results on fluvial systems.

2. Conceptual framework for examining the geomorphic impacts of animals

The geomorphic actions of animals can be categorized into several related groups (Fig. 1, adapted from Hall and Lamont, 2003): trampling, which also encompasses wallowing; loading of slopes by the weight of animals; burrowing and denning; digging for food; dam construction by beavers (Butler and Malanson, 1995, 2005); and *lithophagy* and *geophagy*, or feeding on rock and soil materials, respectively. The latter two actions tend to be highly localized and limited in spatial extent, although geophagy at salt licks in concert with trampling can produce depressions and subsequent ponding (Butler, 1995). The effects of lithophagy and geophagy will not, however, be further considered here.

Hall and Lamont's diagram (Fig. 1) illustrates the linkages and effects of burrowing, digging, trampling, and loading on drainage basins and river/lake catchments. This diagram can be extended into other biogeoclimatic zones and encompass the effects of beaver damming, as shown on Fig. 1. Collectively, the diagram illustrates the profound direct and indirect effects animals have on drainage systems and fluvial landscapes.

3. Direct animal impacts on stream systems

Humans have drastically reduced the geographic range and populations of thousands of species of animals, and, in many notable cases, such as the dodo (*Raphus cucullatus*) and the so-called Tasmanian wolf (*Thylacinus cynocephalus*), driven them to extinction. In the case of extinctions it is impossible to determine what role, if any, a species of animal may have directly had on fluvial systems and indirectly had on surface infiltration, soil moisture retention, soil compaction, and runoff. In some cases, however, the geomorphic effects can be examined and measured for a species whose range and population have been restricted as a result of exploration and population expansion associated with European colonization. A complete list and examination of such cases is far beyond the scope of this paper, and readers are referred to Butler's (1995) text on the geomorphic role of animals.

Human colonization and population growth associated with the period of European expansion did not, of course, only lead to the reduction in geomorphically active native animals. It also created profound, and at times confounding, geomorphic influences on stream systems and hydrology by introducing non-native species into new ecoregions where they subsequently escaped and flourished, a result of an absence of natural predators and in some cases competitive advantages over native species in the same region. The examples are legion, and the economic impacts are staggering (Pimentel et al., 2000; Dukes and Mooney, 2004; Edwards et al., 2004). In spite of the widespread dispersal of feral animals, however,

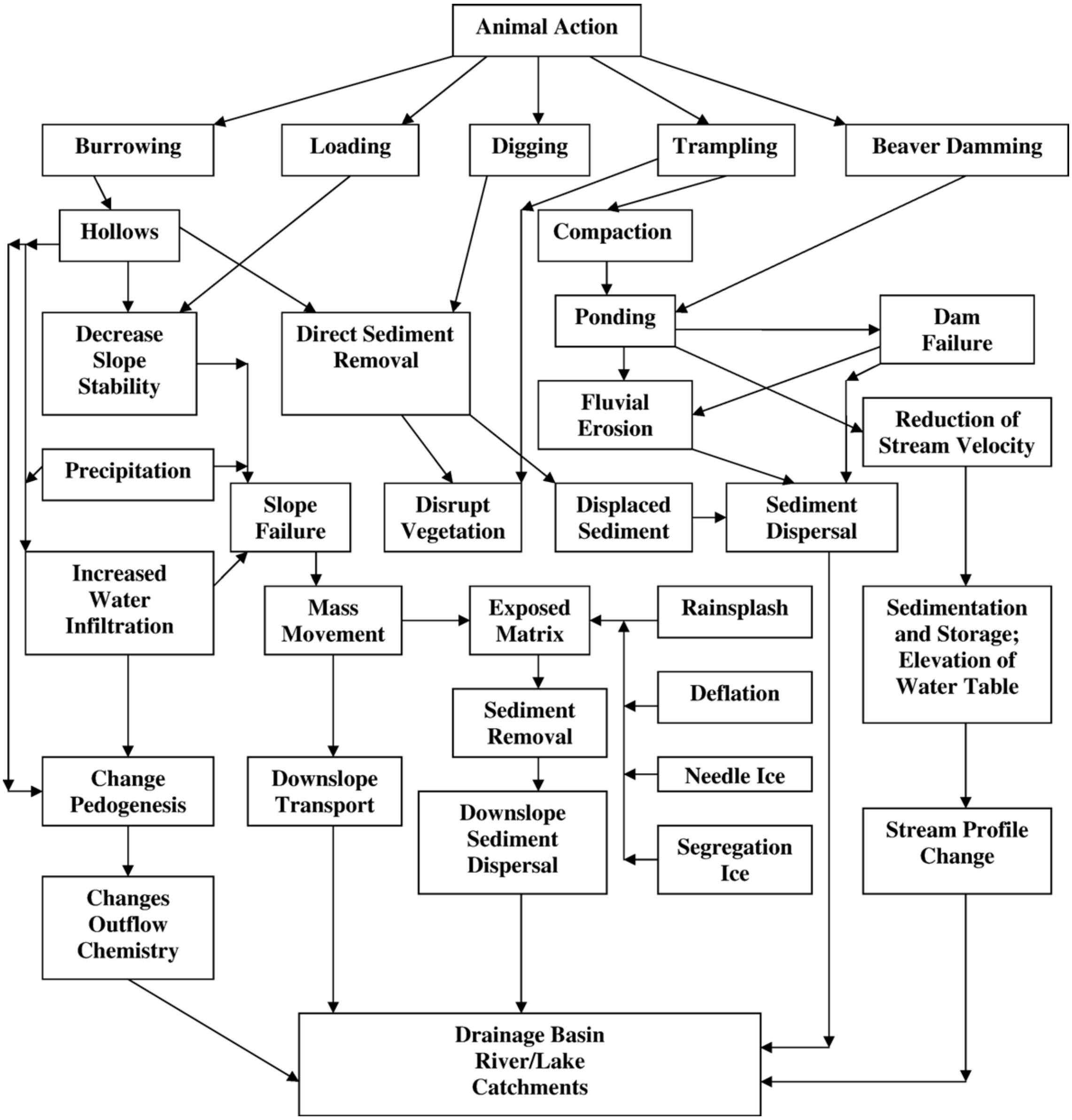

Fig. 1. Conceptual diagram of the geomorphic effects of animals on drainage basins and hillslopes, adapted from Hall and Lamont (2003).

they remain little studied. Several examples from the literature are presented here in a subsequent section.

3.1. Geomorphic effects of free-ranging, natural animal populations and the corresponding effects of range and population reduction

Beavers historically had a greater influence on stream systems than any other animal in North America or Europe, with the Canadian beaver (*Castor canadensis*) being particularly well studied. The Canadian beaver is a large (adult mass > 15 kg; Butler, 1995), semiaquatic rodent whose primary geomorphic role is the damming of streams with subsequent creation of ponds, elevation of water tables, and reduction of stream velocities and induced sedimentation (Marston, 1994; Butler and Malanson, 1995; Meentemeyer and Butler, 1999; Bigler et al., 2001; Butler and Malanson, 2005) (Fig. 1). Secondary geomorphic effects on stream systems are created through the excavation of bank burrows, streamside slides, and canals (Butler and Malanson, 1994; Meentemeyer et al., 1998). A beaver dam can fail catastrophically and result in a flood wave and extreme scouring downstream (Butler, 1989; Marston, 1994;

Gurnell, 1998; Hillman, 1998; Cenderelli, 2000; Butler and Malanson, 2005).

The geomorphic effects of beavers on the landscape have been described from a variety of landscapes across North America, ranging from mountainous terrain (Butler and Malanson, 1994, 1995; Bigler et al., 2001), to the subarctic (Woo and Waddington, 1990; Lewkowicz and Coultish, 2004), to disparate sites in the interior of the Canadian Shield (Naiman et al., 1988), to floodplains and deltaic tidal marshes along the eastern coast of the United States (Townsend and Butler, 1996; Pasternack, 2001). Naiman et al. (1988) emphasized the widespread significance of beavers to the pre-contact fluvial landscape, noting that streams with beaver ponds offer greater resistance to floods, and that streams with beavers return to predisturbance conditions more rapidly than on streams without beavers.

Most recently, Butler and Malanson (2005) described the quantitative effects of the near-extirpation of the beaver during the period following European contact and expansion across North America. They showed that although modern beaver ponds entrap hundreds of millions to a few billion cubic meters of sediment, these values pale in significance compared to the values associated with beavers on the pre-contact landscape when beaver ponds entrapped hundreds of billions of cubic meters of sediment. Widespread removal of North American beavers via trapping for fur led to increased stream incision, attendant changes from relatively clear-flowing to sediment-laden streams, and pronounced changes in the riparian environments of North American stream systems that are still being experienced in the 21st Century (an excellent discussion of the effects of the removal of beaver from western North American rivers may be found in Wohl, 2001).

Hall and Lamont's (2003) conceptual model (Fig. 1) for the role of animals as geomorphic agents did not originally mention beavers and damming, because their work was carried out in the treeless landscape of the Canadian alpine zone. The simple addition of another category of effects, entitled "beaver damming", with subsequent effects, easily accommodates the geomorphic role of beavers.

Naiman (1988) provided a general overview of the impacts of large animals on ecological systems, and commented that grazing animals, such as elephants, have substantial impacts on the structure and dynamics of riparian zones. Naiman and Rogers (1997) subsequently expanded on Naiman's ideas, and provided specific photographs of trails and wallows in riparian zones created by large mammals, such as elephants, hippopotami, and water buffalo. They noted that the combined ecological and geomorphic impacts of large animals can significantly modify the structure and function of African river corridors, and suggested that large ungulates (moose, deer, and elk) may serve similar functions in North American riparian corridors.

3.2. Geomorphic effects of introduced feral animals

Few studies exist that describe the geomorphic effects of feral animals, except within the context of grazing species, such as cattle, sheep, and goats (c.f. Bowman and Panton, 1991; Moles, 1992; Evans, 1998; Oostwoud Wijdenes et al., 2000, 2001; Mieth and Bork, 2005). Pickard (1999) provided one of the few detailed geomorphic examinations of the effects of feral rabbits (described further in a subsequent section), in his study of tunnel erosion in gypsum in a semi-arid portion of New South Wales, Australia. He illustrated that rabbit burrows excavated in an area of gypsum bedrock capture runoff in a fashion similar to karst swallowholes; the burrows subsequently expand and collapse to form holes up to 3 m in diameter and 1.8 m deep. The infrequent surface floodwaters drain down the burrows and create a network of gypsum karst tunnels that flow, in turn, into abandoned human mines underneath the warrens. Quantitative values on the amount of water drained into such systems have not been published.

4. Indirect impacts by animals on stream systems through impacts on basin hydrology and sediment loads

4.1. Geomorphic effects of free-ranging, natural animal populations and the corresponding effects of range and population reduction

4.1.1. North American bison

The North American bison (*Bison bison*) (Figs. 2, 3), often mistakenly called a "buffalo," is a large, herd-dwelling herbivore that numbered from 30 to 60 million prior to European contact (Knapp et al., 1999). Prior to contact, bison ranged across the grasslands of central North America, but also foraged well into the southeastern United States (Rostlund, 1960; De Vorsey, 2001). The replacement of bison with cattle was described in several chapters in *Man's Role in Changing the Face of the Earth* (Bates, 1956; Clark, 1956; Curtis, 1956), but only descriptively and with no attention to the different geomorphic impacts bison herds have on the landscape in comparison to cattle. Utilizing the Hall and Lamont (2003) conceptual model (Fig. 1), bison herds impact the landscape through trampling and wallowing, as well as by

Fig. 2. Bison in so-called “buffalo wallow” in shortgrass prairie, Waterton Lakes National Park, southwestern Alberta, Canada.

loading of slopes. The latter activity has not been described in detail for bison, and is not examined further here.

Trampling effects of bison can be subdivided into wallowing and non-wallowing activity. Wallows are roughly circular depressions created by bison pawing the ground and repeatedly rolling in exposed soil (Fig. 2) (Coppedge et al., 1999; Knapp et al., 1999). Wallowing is a behavior not employed by cattle, and, thus, the removal of bison had profound geomorphic implications not considered in *Changing the Earth*. Wallows are typically 2–10 m in diameter and 10–30 cm deep (Knapp et al., 1999; McMillan, 1999). To calculate the amount of material excavated from a typical wallow, circularity was assumed, and area was calculated using the formula πr^2. For a range in radii of 1–5 m, area of wallows are calculated as 3.14 m^2–78.5 m^2. Assuming an *average* depth of 10–30 cm, a 1-m radius wallow accounts for *ca.* 0.3 m^3–0.9 m^3 of sediment displaced. For a wallow with a 5-m radius and an average depth of 10–30 cm, 7.8 m^3–23.5 m^3 of sediment is removed, although compaction via wallowing accounts for some of the apparent below-surface loss. Bulk density of soil in wallows, as a result of rolling and trampling, is significantly greater than the adjacent landscape. McMillan (1999) cites a density increase of 17% relative to adjacent tallgrass prairie. The compaction reduces infiltration, so that wallows serve as local ponds that can retain water for several days following a rainstorm (Knapp et al., 1999; McMillan, 1999). The number of pre-contact wallows has been estimated at more than 100 million, comprising over 80,000 ha in the tallgrass prairie alone (McMillan, 1999). The influence that over 100 million bison wallows in the tallgrass prairie, and perhaps an equal combined number in the mid- and shortgrass prairies, had on surface hydrology and runoff can only be considered to have been regionally substantial and locally enormous.

Bison grazing and trampling that accompanied grazing have been credited with holding back aspen expansion in the northern plains (Campbell et al., 1994), maintaining shortgrass prairie in areas where mid-grass prairie would have otherwise become established (England and DeVos, 1969), and mobilizing sand dune fields in the Great Plains during periods of protracted drought (Forman et al., 2001). Each of these grazing- and/or trampling-induced results has obvious ramifications on soil infiltration, surface runoff, and erosion. Bison trampling and slope loading along stream channels also led to the creation of well-established trails on the plains that led to stream crossings (Butler, 1995). Bison further altered stream habitats by locally increasing the silt fraction of the streambed and widening stream channels at crossing points (Fritz et al., 1999) (Fig. 3).

Bison grazing in the Great Plains had an additional zoogeomorphic impact of great import: mixed-grass prairie vegetation was kept sufficiently short so that prairie dogs could colonize the area (Hygnstrom and Virchow, 2002). Prairie dogs are herbivorous, colonial rodents that create large burrow systems (Fig. 4) (Whicker and Detling, 1988). Prairie dog burrowing and grazing in turn positively interacts with, and, therefore, encourages additional bison grazing (Whicker and Detling, 1988), resulting in a feedback of additional bison trampling and wallowing.

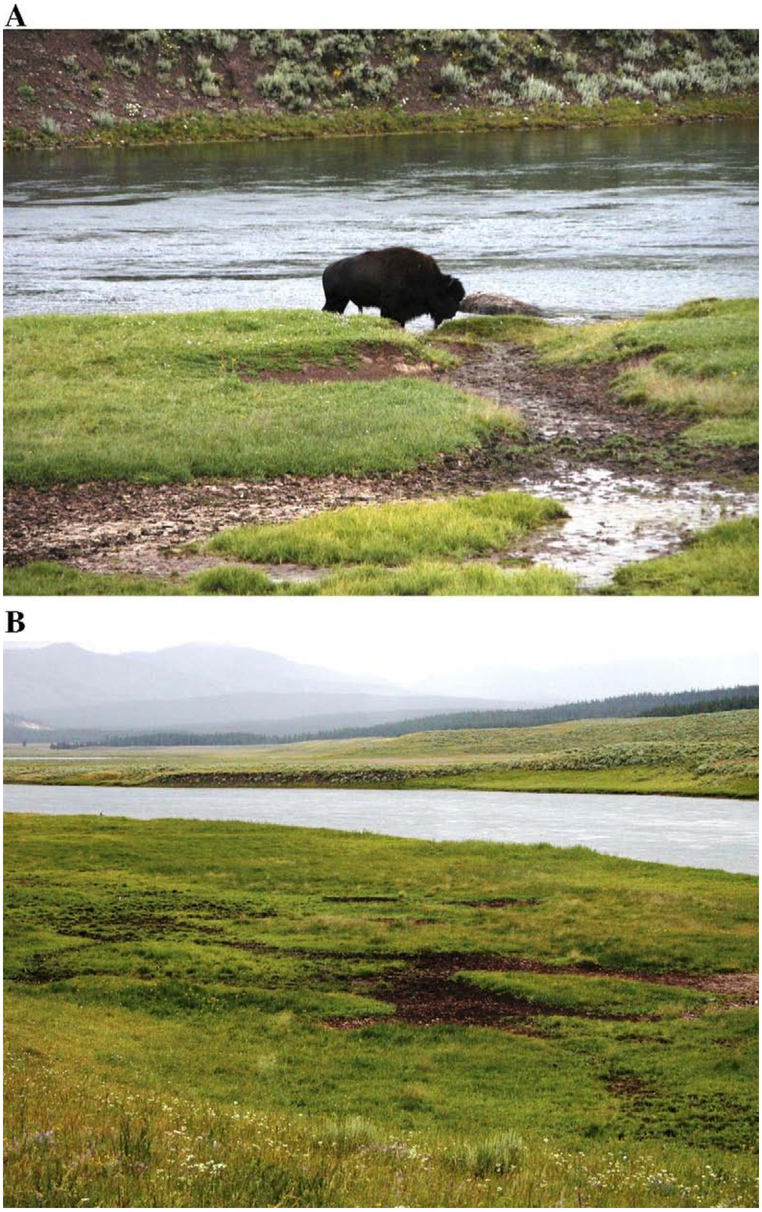

Fig. 3. Bison trampling along the banks of the Yellowstone River, Yellowstone National Park, Wyoming, USA; A) Bison emerging from the river at heavily trampled pathway. B) Heavily trampled sites on both banks of Yellowstone River caused by bison.

4.1.2. Prairie dogs

The black-tailed prairie dog (*Cynomys ludovicianus*) is the most widely distributed of five native species of prairie dogs in North America (Hygnstrom and Virchow, 2002), and has been the subject of the greatest amount of research concerning effects on soils, drainage, and local hydrology. Black-tailed prairie dogs were widespread throughout the mixed- and short-grass prairies of North America, ranging from southern Canada to northern Mexico, and from the foothills of the Rockies eastward to approximately 98° W longitude (Hygnstrom and Virchow, 2002); other species of prairie dogs occupy other western US states including California, Oregon, Washington, and Idaho. Modern species have occupied the Great Plains since at least the late Pleistocene (Lomolino and Smith, 2003), and additional extinct Pleistocene species left behind burrow casts that suggest that they occupied similar ecological niches with similar geomorphic tendencies (Young et al., 1999). In general, the overall range of the prairie-dog was apparently relatively stable over the past 40,000 years

Fig. 4. Typical entrance to a prairie-dog burrow in Devils Tower National Monument, northeastern Wyoming, USA. Note the associated sediment mound with 49-mm lens cap for scale.

until European Contact (Lomolino and Smith, 2001). Over 40 million hectares of the prairie region were occupied by black-tailed prairie dogs in the early 1900s (Senseman et al., 1994), an area representing more than 20% of the natural short- and mixed-grass prairies (Whicker and Detling, 1988). Since the early 1900s, the range of the prairie-dog has been reduced to less than 600,000 ha by eradication efforts associated with American agriculture (Lomolino et al., 2003). In Texas alone, historic populations of black-tailed prairie dogs were estimated in the early 20th Century at 800 million individuals occupying over 230,000 km^2; eradication efforts and land-use changes have reduced the Texas population by greater than 99% (Weltzin et al., 1997).

The geomorphic effects of prairie dogs occur via the “burrowing” pathways illustrated by Hall and Lamont (2003) (Fig. 1), and include creation of hollows, direct sediment removal, changes in pedogenesis, increased water infiltration, changes in outflow chemistry, and downslope sediment dispersal (Whicker and Detling, 1988; Day and Detling, 1994); all of which have implications for drainage systems. A typical prairie-dog burrow system has two entrances, is *ca.* 1–3 m deep, *ca.* 15 m long, and has a diameter of 10–13 cm. Each burrow system mixes *ca.* 200–225 kg of soil, much of it deposited as mounds around the entrances, with 50–300 burrow entrances per hectare (Whicker and Detling, 1988).

The data provided per burrow system and hectare by Whicker and Detling (1988) allow for some illuminating extrapolations of the number and scale of geomorphic impacts of prairie dogs in pre-Contact time. Assume, if each burrow system has one or two entrances, and that 50–300 burrow entrances per hectare exist, each hectare occupied by pre-Contact prairie dogs contained 25–300 burrow systems. If each burrow system mixes 200–225 kg of soil; and 25 systems exist per hectare, each hectare has 5000–5625 kg of soil mixed by prairie dogs, with attendant effects on the surface hydrology and sediment movement of that hectare. If, on the other hand, 300 systems occur per hectare, with 200–225 kg of soil mixed per each hectare, then each hectare occupied undergoes 60,000–67,500 kg of soil mixing by prairie dogs. Considering that prairie dogs currently occupy only about 1.5% of the pre-Contact range, it seems safe to say that an enormous zoogeomorphic influence on the hydrology of the Great Plains region was removed by the efforts to eradicate prairie dogs.

4.1.3. Grizzly bears

Grizzly bears (*Ursus arctos horribilis*), once found throughout the Rocky Mountains and indeed eastward across the northern High Plains, numbered in the tens of thousands (Butler, 1992). Today, they are restricted to six “ecosystems” in Wyoming, Montana, Idaho, and Washington in the lower 48 United States; numbers and distributions are higher in Alaska as well as in British Columbia and Alberta, Canada. Fewer than 2000 grizzlies remain in the “lower 48”.

The grizzly bear is a large omnivore. Adult bears are 160 kg or more in bodyweight and stand 1.25 m at the shoulder (Butler, 1992). Grizzlies dig for plant and animal sources of food (Holcroft and Herrero, 1984; Edge et al., 1990; Butler, 1992; Mattson, 1997; Mattson and Reinhart, 1997; Tardiff and Stanford, 1998; Hall et al., 1999; Baer and Butler, 2000; Hall and Lamont, 2003), annually excavate hibernation dens (Butler, 1992, 1995; Hall and Lamont, 2003), and load slopes (*sensu*Hall and Lamont, 2003). Each of these major categories of geomorphic activity can result in direct sediment removal and dispersal into drainage basins, causing direct and indirect effects on fluvial systems (Fig. 1).

The geomorphic impacts of grizzly bears on slope hydrology and fluvial systems is seasonally distinct (Baer and Butler, 2000). During early spring, grizzlies dig for tubers in riparian corridors and introduce sediment into streams already swollen with spring runoff. Grizzlies excavate broad areas in the search for roots and tubers, and may also cache carrion carried into stream bottoms by snow avalanches during the previous winter (Butler, 1995; Baer and Butler, 2000).

In summer months, geomorphically significant excavations occur in the subalpine and alpine zones near treeline as grizzlies migrate upward in search of food and relief from heat. Individual excavations for glacier lily (*Erythronium grandiflorum*) bulbs (Fig. 5), yellow sweetvetch (*Hedysarum sulphurescens*) roots, and biscuitroots (*Lomatium cous*) may cover an area greater than 75 × 25 m, directly causing sediment displacement and indirectly affecting soil compaction and rates of infiltration (Fig. 1). During the summer, bears also attempt to excavate rodents and insects on hillslopes, causing additional sediment displacement and affecting slope hydrology and runoff (Butler, 1995, and references therein). In late summer the bears descend to seek out wild berries on lower hillslopes, but they ascend again as autumn gives way to winter (typically in mid-late October at latitudes of 45 to 50° north) to excavate winter dens. Dens are typically excavated near upper treeline on steep hillslopes averaging 30–35° (Butler, 1992; Baer and Butler, 2000). New dens must be excavated each year, as spring snowmelt and summer rains cause the dens to collapse and the sediments are flushed downslope and into adjacent streams. Each den annually displaces *ca.* 4–5 m^3 into the hillslope debris cascade.

Butler (1992) previously estimated, through conservative estimates of the number of food excavations combined with den excavations, that a minimum of 1350 m^3 was displaced downslope annually by an estimated population of 200 grizzly bears in Glacier Park, Montana. Recent studies in Glacier National Park revealed that population estimates of grizzly bears have undercounted the true number of bears (U.S.G.S., 2000). Results of DNA analysis of hair snags and fecal samples indicate a population of 241 to 549 grizzlies, with 332 bears the preferred figure. Using this new population estimate, a minimum of 2249 m^3 of annual sediment displacement occurs in Glacier Park from grizzly bear excavations, with attendant direct and indirect impacts on the hydrology of park hillslopes and adjacent fluvial systems. Quantitative estimates of the amount of sediment displaced and dispersed downslope have also been provided for areas in the Canadian Rockies by Hall et al. (1999) and Hall and Lamont (2003). The reduction of the geographic range of grizzlies has removed these powerful geomorphic agents, and influence on fluvial systems and sediment budgets, from well over 95% of the pre-European-contact range in the lower 48 states of the USA.

4.2. Indirect geomorphic effects of introduced feral animals

4.2.1. Feral rabbits

Although the study of the geomorphic impacts of native animal species on the Australian landscape is an area of increasing interest (e.g., Bennett, 1999; Eldridge and Rath, 2002), the impacts of native species on the Australian landscape has been overshadowed by research

Fig. 5. Area excavated by grizzly bear in search of tubers and roots. Note the 49 mm lens cap for scale.

on the impacts of non-native species (Edwards et al., 2004), including the European rabbit (*Oryctolagus cuniculus* L.). Feral rabbits have excavated widespread warrens across the semi-arid landscape of Australia, and in the process removed vegetation, created mounds, and compacted soils (Eldridge and Myers, 2001; Eldridge and Simpson, 2002). Pressures from rabbit grazing have also profoundly altered the vegetation of Australian rangelands, where perennial pasture species have been replaced by annuals (Edwards et al., 2004), in turn producing largely unmeasured effects on Australian hydrology and sediment dispersal. The geomorphic effects of feral rabbits are conceptually illustrated along Hall and Lamont's (2003) "burrowing" and "trampling" pathways (Fig. 1), all of which have ramifications for water infiltration, sediment dispersal, and effects on drainage basins.

In spite of the widespread deleterious impacts of overgrazing and digging by European rabbits on the Australian landscape, however, very few specific studies have been carried out on the direct geomorphic impacts (as contrasted to the commonly studied impacts on vegetation and soils). Eldridge and Myers (2001) examined the impact of extensive rabbit warrens on soil and ecological processes, and described the specific geomorphology of the warrens. They described microsurface features including scarps, flat inter-mound surfaces, and depressions, and noted that mounds surrounding warren entrances were characterized by large internal depressions that resulted from collapse of burrow entrances (Eldridge and Myers, 2001, p. 333). Although they did not describe the effects such warrens must have on surface drainage, obviously warrens act as conduits into subsurface drainage systems rather than allowing surface runoff.

4.2.2. Feral burros and horses

Feral burros and horses are pests with significant geomorphic impacts in the western United States and in Australia (Symanski, 1994; Pimentel et al., 2000; Dukes and Mooney, 2004; Edwards et al., 2004), although data on specific numbers of each are controversial (Symanski, 1994). Feral burros, *Equus asinus*, and feral horses (*Equus caballus*) are common animals in many areas of the American southwest (Hanley and Brady, 1977; Pimentel et al., 2000) as well as in Australian rangelands (Edwards et al., 2004). They graze on, and drastically reduce, native vegetation so that native perennials are replaced by annuals. The grazing also reduces the overall surface vegetation cover and exposes a greater area to raindrop impact, surface runoff, and sediment dispersal (Hanley and Brady, 1977). They also presumably contribute to widespread erosion (Edwards et al., 2004) via the "trampling" process as illustrated schematically by Hall and Lamont (2003) (Fig. 1). These direct erosional impacts, as well as the secondary erosional impacts attributable to vegetation cover change and overall reduction of vegetation, have been qualitatively observed but are completely unquantified in the geomorphic literature.

Fig. 6. Area trampled and rooted by feral hogs, central Texas, USA. Photo courtesy of Ellen Cagle.

4.2.3. Feral pigs

Feral pigs or hogs (*Sus scrofa*) are widespread in many habitats around the world, including such diverse locations as the humid eastern and semi-arid western United States (Kotanen, 1995; Pimentel et al., 2000; Sweitzer and Van Vuren, 2002; Dukes and Mooney, 2004), tropical Malaysia (Ickes et al., 2001), tropical and semi-arid Australia (Friend and Cellier, 1990; Bowman and Panton, 1991; Edwards et al., 2004), and subarctic Sweden (Welander, 2000). The impacts on native vegetation have profound implications for secondary geomorphic effects via grazing and associated alteration in surface vegetation cover. They also create primary geomorphic impacts via pathways (Hall and Lamont, 2003) of trampling and uprooting of soil (Fig. 6). In California, USA, for example, feral pigs are now the primary agents of soil disturbance in some grasslands (Kotanen, 1995; Dukes and Mooney, 2004). Areas of disturbance created by soil rooting by feral pigs range from 2–3.6% in Australia, up to 13% in Poland, and between 6–11% in Hawaii (Welander, 2000). As much as 80% of the forest floor may be rooted by feral pigs in humid forests of the U.S. Appalachians (Welander, 2000), and parts of California have an areal disturbance of over 7% annually (Kotanen, 1995). Uprooting by pigs subject surface sediment to aeolian and fluvial dispersal, and pig trampling at river crossings can induce bank destabilization and erosion (Edwards et al., 2004). The mixing of soil caused by pig uprooting should produce distinct micro-site variability in infiltration and runoff; published quantitative data for such impacts do not, unfortunately, currently exist. Nevertheless, given the widespread spatial extent of pig uprooting, and the attendant effects on surface vegetation, soils, and sediments, feral pigs have profound geomorphic impacts that did not exist prior to introduction. Quantitative confirmation of this statement awaits future geomorphological research.

5. Concluding remarks

Humans have profoundly altered the geomorphic impacts of animals on fluvial and hydrologic systems through the reduction of geomorphically active native species, such as beavers, bears, bison, and prairie dogs; and by the introduction of animals that subsequently became feral and geographically widespread. The varying geomorphic impacts of native versus feral animals may cancel each other out, although that is unlikely given the different geomorphic influences of many of these animals, changes in the geographic distributions of species, and human land-use changes that greatly restrict some animal impacts (e.g. bison and prairie dogs) while not strongly altering others (e.g., feral pigs). The collective geomorphic impacts of native and introduced animals have had profound implications for spatial and temporal changes in fluvial systems. Geomorphologists have been slow to recognize the role of animals on fluvial systems, and even slower to recognize how those roles have changed through time in the post-European Contact era. It is already too late to truly quantify the geomorphic impact of pre-Contact bison or beaver; extrapolations back through time are only simplified estimates of the potential geographic extent, variability, and magnitude of impacts such animals had. Geomorphologists would be well advised to learn the lessons of the past, and initiate a broad program of measurements of the geomorphic impacts of current animals before those impacts also change because of human impact, overpopulation, and global climate change.

Acknowledgements

I thank L. Allan James and W. Andrew Marcus for their editorial assistance; two anonymous referees for the excellent comments that substantially improved the focus of the paper; Ellen Cagle for sharing her photographs of her master's research on feral hogs and their geomorphic and biogeographic impacts in central Texas; and my family for participating in (and putting up with) my desire for photographic documentation of the geomorphic impacts of animals.

References

Baer, L.D., Butler, D.R., 2000. Space-time modeling of grizzly bears. The Geographical Review 90 (2), 206–221.

Bates, M., 1956. Man as an agent in the spread of organisms. In: Thomas Jr., W.L. (Ed.), Changing the Face of the Earth. University of Chicago Press, Chicago, pp. 788–804.

Bennett, M.B., 1999. Foot areas, ground reaction forces and pressures beneath the feet of kangaroos, wallabies and rat–kangaroos (Marsupialia: Macropodoidea). Journal of the Zoological Society of London 247, 365–369.

Bigler, W., Butler, D.R., Dixon, R.W., 2001. Beaver-pond sequence morphology and sedimentation in northwestern Montana. Physical Geography 22 (6), 531–540.

Bowman, D.M.J.S., Panton, W.J., 1991. Sign and habitat impact of banteng (*Bos javanicus*) and pig (*Sus scrofa*), Cobourg Peninsula, northern Australia. Australian Journal of Ecology 16 (1), 15–17.

Butler, D.R., 1989. The failure of beaver dams and resulting outburst flooding: a geomorphic hazard of the southeastern Piedmont. The Geographical Bulletin 31, 29–38.

Butler, D.R., 1992. The grizzly bear as an erosional agent in mountainous terrain. Zeitschrift für Geomorphologie 36 (2), 179–189.

Butler, D.R., 1995. Zoogeomorphology — Animals as Geomorphic Agents. Cambridge University Press, Cambridge, UK. 231 pp.

Butler, D.R., Malanson, G.P., 1994. Canadian landform examples — beaver landforms. The Canadian Geographer 38 (1), 76–79.

Butler, D.R., Malanson, G.P., 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. Geomorphology 13 (1–4), 255–269.

Butler, D.R., Malanson, G.P., 2005. The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71 (1–2), 48–60.

Campbell, C., Campbell, I.D., Blyth, C.B., McAndrews, J.H., 1994. Bison extirpation may have caused aspen expansion in western Canada. Ecography 17 (4), 360–362.

Cenderelli, D.A., 2000. Floods from natural and artificial dam failures. In: Wohl, E.E. (Ed.), Inland Flood Hazards: Human, Riparian and Aquatic Communities. Cambridge University Press, Cambridge, pp. 73–103.

Clark, A.H., 1956. The impact of exotic invasion on the remaining New World mid-latitude grasslands. In: Thomas Jr., W.L. (Ed.), Changing the Face of the Earth. University of Chicago Press, Chicago, pp. 737–762.

Coppedge, B.R., Fuhlendorf, S.D., Engle, D.M., Carter, B.J., Shaw, J.H., 1999. Grassland soil depressions: relict bison wallows or inherent landscape heterogeneity? American Midland Naturalist 142 (2), 382–392.

Curtis, J.T., 1956. The modification of mid-latitude grasslands and forests by man. In: Thomas Jr., W.L. (Ed.), Changing the Face of the Earth. University of Chicago Press, Chicago, pp. 721–736.

Day, T.A., Detling, J.K., 1994. Water relations of *Agropyron smithii* and *Bouteloua gracilis* and community evapotranspiration following long-term grazing by prairie dogs. American Midland Naturalist 132 (2), 381–392.

De Vorsey Jr., L., 2001. Searching for William Bartram's buffalo lick. The Southeastern Geographer 41 (2), 159–183.

Dukes, J.S., Mooney, H.A., 2004. Disruption of ecosystem processes in western North America by invasive species. Revista Chilena de Historia Natural 77, 411–437.

Edge, W.D., Marcum, C.L., Olson-Edge, S.L., 1990. Distribution and grizzly bear, *Ursus arctos*, use of yellow sweetvetch, *Hedysarum sulphurescens*, in northwestern Montana and southeastern British Columbia. Canadian Field-Naturalist 104 (3), 435–438.

Edwards, G.P., Pople, A.R., Saalfeld, K., Caley, P., 2004. Introduced mammals in Australian rangelands: future threats and the role of monitoring programmes in management strategies. Austral Ecology 29 (1), 40–50.

Eldridge, D.J., Myers, C.A., 2001. The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. Journal of Arid Environments 47, 325–337.

Eldridge, D.J., Rath, D., 2002. Hip holes: kangaroo (*Macropus* spp.) resting sites modify the physical and chemical environment of woodland soils. Austral Ecology 27, 527–536.

Eldridge, D.J., Simpson, R., 2002. Rabbit (*Oryctolagus cuniculus* L.) impacts on vegetation and soils, and implications for management of wooded rangelands. Basic and Applied Ecology 3 (1), 19–29.

England, R.E., DeVos, A., 1969. Influence of animals on pristine conditions on the Canadian grasslands. Journal of Range Management 22, 87–94.

Evans, R., 1998. The erosional impacts of grazing animals. Progress in Physical Geography 22 (2), 251–268.

Forman, S.L., Oglesby, R., Webb, R.S., 2001. Temporal and spatial patterns of Holocene dune activity on the Great Plains of North America: megadroughts and climate links. Global and Planetary Change 29 (1), 1–29.

Friend, G.R., Cellier, K.M., 1990. Wetland herpetofauna of Kakadu National Park, Australia: seasonal richness trends, habitat preferences and the effects of feral ungulates. Journal of Tropical Ecology 6, 131–152.

Fritz, K.M., Dodds, W.K., Pontius, J., 1999. The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. American Midland Naturalist 141, 253–265.

Gurnell, A.M., 1998. The hydrogeomorphological effects of beaver dam-building activity. Progress in Physical Geography 22, 167–189.

Hall, K., Lamont, N., 2003. Zoogeomorphology in the Alpine: some observations on abiotic–biotic interactions. Geomorphology 55 (1–4), 219–234.

Hall, K., Boelhouwers, J., Driscoll, K., 1999. Animals as erosion agents in the alpine zone: some data and observations from Canada, Lesotho, and Tibet. Arctic, Antarctic, and Alpine Research 31 (4), 436–446.

Hanley, T.A., Brady, W.W., 1977. Feral burro impact on a Sonoran Desert range. Journal of Range Management 30 (5), 374–377.

Hillman, G.R., 1998. Flood wave attenuation by a wetland following a beaver-dam failure on a second order boreal stream. Wetlands 18, 21–34.

Holcroft, A.C., Herrero, S., 1984. Grizzly bear digging sites for *Hedysarum sulphurescens* roots in southwestern Alberta. Canadian Journal of Zoology 62, 2571–2575.

Hygnstrom, S.E., Virchow, D.R., 2002. Prairie Dogs and the Prairie Ecosystem. University of Nebraska School of Natural Resources, Lincoln, NE. 8 pp.

Ickes, K., Dewalt, S.J., Appanah, S., 2001. Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. Journal of Tropical Ecology 17, 191–206.

Knapp, A.K., Blair, J.M., Briggs, J.M., Collins, S.L., Hartnett, D.C., Johnson, L.C., Towne, E.G., 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49 (1), 39–50.

Kotanen, P.M., 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. Ecography 18, 190–199.

Lewkowicz, A.G., Coultish, T.L., 2004. Beaver damming and palsa dynamics in a subarctic mountainous environment, Wolf Creek, Yukon Territory, Canada. Arctic, Antarctic, and Alpine Research 36 (2), 208–218.

Lomolino, M.V., Smith, G.A., 2001. Dynamic biogeography of prairie dog (*Cynomys ludovicianus*) towns near the edge of their range. Journal of Mammalogy 82 (4), 937–945.

Lomolino, M.V., Smith, G.A., 2003. Prairie dog towns as islands: applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates. Global Ecology and Biogeography 12, 275–286.

Lomolino, M.V., Smith, G.A., Vidal, V., 2003. Long-term persistence of prairie-dog towns: insights for designing networks of prairie reserves. Biological Conservation 115, 111–120.

Marston, R.A., 1994. River entrenchment in small mountain valleys of the western USA: influence of beaver, grazing and clearcut logging. Revue de Geographie de Lyon 69, 11–15.

Mattson, D.J., 1997. Selection of microsites by grizzly bears to excavate biscuitroots. Journal of Mammalogy 78 (1), 228–238.

Mattson, D.J., Reinhart, D.P., 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. Journal of Applied Ecology 34, 926–940.

McMillan, B.R., 1999. Bison Wallowing and Its Influence on the Soil Environment and Vegetation Characteristics in Tallgrass Prairie. Unpublished Doctoral Dissertation, Kansas State University, Manhattan, KS.

Meentemeyer, R.K., Butler, D.R., 1999. Hydrogeomorphic effects of beaver dams in Glacier National Park, Montana. Physical Geography 20 (5), 436–446.

Meentemeyer, R.K., Vogler, J.B., Butler, D.R., 1998. The geomorphic influences of burrowing beavers on streambanks, Bolin Creek, North Carolina. Zeitschrift für Geomorphologie 42 (4), 453–468.

Mieth, A., Bork, H.-R., 2005. History, origin and extent of soil erosion on Easter Island (Rapa Nui). Catena 63, 244–260.

Moles, R., 1992. Trampling damage to vegetation and soil cover at paths within the Burren National Park, Mullach Mor, Co. Clare. Irish Geography 25 (2), 129–137.

Naiman, R.J., 1988. Animal influences on ecosystem dynamics. BioScience 38 (11), 750–752.

Naiman, R.J., Rogers, K.H., 1997. Large animals and system-level characteristics in river corridors. BioScience 47 (8), 521–529.

Naiman, R.J., Johnston, C.A., Kelley, J.C., 1988. Alteration of North American streams by beaver. BioScience 38, 753–762.

Oostwoud Wijdenes, D.J., Poesen, J., Vandekerckhove, L., Kosmas, C., 2000. The use of marked rock fragments as tracers to assess rock fragments transported by sheep trampling on Lesvos, Greece. In: Foster, Ian D.L. (Ed.), Tracers in Geomorphology. John Wiley & Sons Ltd., Chichester, U.K., pp. 201–220.

Oostwoud Wijdenes, D.J., Poesen, J., Vandekerckhove, L., Kosmas, C., 2001. Measurements at one-year interval of rock-fragment fluxes by sheep trampling on degraded rocky slopes in the Mediterranean. Zeitschrift für Geomorphologie 45 (4), 477–500.

Pasternack, G.B., 2001. Animal response to river evolution in the tidal freshwater zone. In: Dorava, Joseph M., Montgomery, David R., Palcsak, Betty B., Fitzpatrick, Faith A. (Eds.), Geomorphic Processes and Riverine Habitat (Water Science and Application 4). American Geophysical Union, Washington, D.C., pp. 139–157.

Pickard, J., 1999. Tunnel erosion initiated by feral rabbits in gypsum, semi-arid New South Wales, Australia. Zeitschrift für Geomorphologie 43 (2), 155–166.

Pimentel, D., Lach, L., Zuniga, R., Morrison, D., 2000. Environmental and economic costs on nonindigenous species in the United States. Bioscience 50 (1), 53–65.

Rostlund, E., 1960. The geographic range of the historic bison in the southeast. Annals of the Association of American Geographers 50 (4), 395–407.

Seagle, S.W., 2003. Can ungulates foraging in a multiple-use landscape alter forest nitrogen budgets? Oikos 103 (1), 230–234.

Seagle, S.W., Liang, S.-Y., 2001. Application of a forest gap model for prediction of browsing effects on riparian forest succession. Ecological Modelling 144 (2–3), 213–229.

Senseman, G.M., Nellis, M.D., Robel, R.J., 1994. Spatial analysis of SPOT HRV digital data for measuring landscape parameters of prairie dog towns in Meade County, Kansas. Geocarto International 9 (2), 45–50.

Sweitzer, R.A., Van Vuren, D.H., 2002. Rooting and foraging effects of wild pigs on tree regeneration and acorn survival in California's oak woodland ecosystems. U.S. Department of Agriculture Forest Service General Technical Report PSW–GTR, vol. 184, pp. 219–231.

Symanski, R., 1994. Contested realities: feral horses in Outback Australia. Annals of the Association of American Geographers 84 (2), 251–269.

Tardiff, S.E., Stanford, J.A., 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology 79 (7), 2219–2228.

Thomas Jr., W.L. (Ed.), 1956. Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, IL.

Townsend, P.A., Butler, D.R., 1996. Patterns of landscape use by beaver on the lower Roanoke River floodplain, North Carolina. Physical Geography 17 (3), 253–269.

U.S. Geological Survey, 2000. The Hair of the Bear: USGS Releases Grizzly Bear Numbers in Glacier National Park. http://biology.usgs.gov/pr/newsrelease/2000/5-18.html.

Welander, J., 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. Journal of the Zoological Society of London 252, 263–271.

Weltzin, J.F., Dowhower, S.L., Heitschmidt, R.K., 1997. Prairie dog effects on plant community structure in southern mixed-grass prairie. The Southwestern Naturalist 42 (3), 251–258.

Whicker, A.D., Detling, J.K., 1988. Ecological consequences of prairie dog disturbances. BioScience 38 (11), 778–785.

Wohl, E.E., 2001. Virtual Rivers. Yale University Press, New Haven, CT.

Woo, M.-K., Waddington, J.M., 1990. Effects of beaver dams on subarctic wetland hydrology. Arctic 43, 223–230.

Young, R.R., Burns, J.A., Rains, R.B., Schowalter, D.B., 1999. Late Pleistocene glacial geomorphology and environment of the Hand Hills region and southern Alberta, related to Middle Wisconsin fossil prairie dog sites. Canadian Journal of Earth Sciences 36, 1567–1581.