North American Beaver (*Castor canadensis*): A Technical Conservation Assessment

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COVER PHOTO CREDIT

North American Beaver (*Castor canadensis*). Photograph courtesy of Kansas Department of Wildlife and Parks.

Summary of Key Components for Conservation of North American Beaver

The North American beaver (*Castor canadensis*) is a semi-aquatic mammal occurring in rivers, streams, lakes, reservoirs, and wetlands across North America. Beavers are unique in their ability to create and modify their habitat by building dams. Because they exert such a strong influence on aquatic and riparian communities, the beaver is considered a keystone species. Although the species currently is considered secure across its range, unregulated fur harvest and habitat destruction caused severe declines or extirpation of beavers by 1900 in many parts of the United States, including much of the USDA Forest Service's (USFS) Rocky Mountain Region (Region 2). At present, beavers are locally common and relatively widespread in Region 2 states. Improved regulation of trapping, protection of wetland habitat, translocation efforts, and natural dispersal and population increase have restored beaver populations where suitable habitat remains in much of its original range. The beaver is classified as a furbearer in all Region 2 states and is managed for commercial harvest, except in Colorado where the state constitution restricts trapping methods. Within Region 2 of the USFS, beaver is designated as a Management Indicator Species (MIS) on the Bighorn, Medicine Bow/Routt, Pike/San Isabel, San Juan, and Shoshone national forests. Biologists use MIS to estimate and monitor the effects of management activities on fish and wildlife species.

The principal threats to beaver populations are habitat destruction and degradation. Human population growth and increasing demands on water resources lead to water storage, diversion, and channelization projects that affect rivers, lakes, and wetlands. Water uses can cause short and long-term effects on beaver habitat by changing seasonal flow regimes and stream morphology, and by causing loss or degradation of riparian vegetation. Intense grazing by wild and domestic ungulates in a riparian zone is also a primary cause of beaver habitat degradation. Although commercial trapping is no longer a threat to the species, depredation trapping to mitigate beaver damage, and illegal shooting and trapping are localized threats.

Despite the lack of quantitative data, beaver populations as a whole in all Region 2 states appear to be stable or increasing. Beavers can cause considerable damage to human structures and economic activities, particularly in agricultural and urban areas. Consequently, beaver presence is not compatible in some areas. However, restoring beaver populations to their maximum viability on public lands is usually desirable because of the beaver's capability to restore and maintain healthy riparian ecosystems. This is especially true on National Forest System lands. USFS units in Region 2 are likely to have areas where incised stream channels, altered streamflow regimes, and degraded riparian vegetation limit the potential for beaver re-establishment. Therefore, preventing further habitat degradation and restoring degraded habitats are key to protecting and restoring beaver populations on National Forest System lands. Conversely, reestablishing beaver may help to restore degraded systems.

Beavers have a relatively low biotic potential due to small litter size and a long juvenile development period. Population matrix models showed that survival of kits (1st year juveniles) and yearlings (2nd year juveniles) is the most critical factor in population viability. Survival of these age classes is partly dependent on the ability of beaver to successfully disperse and recolonize habitats. Beavers are strong dispersers, and populations can recover quickly from local reductions when dispersal corridors are maintained. Key conservation elements for the beaver on National Forest System lands are, therefore, protection and enhancement of aquatic and riparian habitats by management of water resources and riparian vegetation, beaver population enhancement by natural recolonization and transplants where necessary, and proactive management of beaver damage issues.

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INTRODUCTION

This conservation assessment is one of many being produced for the Species Conservation Project being conducted by the USDA Forest Service's (USFS) Rocky Mountain Region (Region 2). The North American beaver (*Castor canadensis*; hereafter, the beaver) is the focus of an assessment because it is designated as a Management Indicator Species (MIS) in several USFS Region 2 administrative units. MIS serve as barometers for the effects of land management on wildlife populations through their use as surrogates to: 1) estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 2.19.19 (a)(1)); and 2) monitor the effects of management activities on species via changes in population trends (36 CFR 2.19.19 (a)(6)). This assessment addresses the biology of the beaver throughout its range and in Region 2. The broad nature of the assessment leads to constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced for the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on current scientific knowledge. Assessment goals limit the scope of the work to critical syntheses of scientific knowledge, discussions of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to prescribe management. Instead, it provides the ecological background upon which managers must based their decisions and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, this assessment discusses management approaches used or recommended elsewhere, and evaluates the success of those approaches that have been implemented.

Scope

This assessment examines the biology, ecology, conservation, and management of beavers with specific reference to the geographic and ecological characteristics of the central and southern Rocky Mountains. Although much of the literature on the species originates from field investigations outside the region, this document places that literature in the ecological and social contexts of the central and southern Rocky Mountains.

In producing this assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. This assessment does not reference all of the vast literature on beavers, nor did we consider all published materials equally reliable. We emphasize refereed literature because it is the accepted standard in science. Non-refereed publications or reports were regarded with greater skepticism, but we chose to use some non-refereed literature when refereed information was unavailable. Unpublished data (e.g., USFS monitoring reports, state agency biologist opinions) were important in estimating the distribution and status of the beaver.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, strong inference, as described by Platt, suggests that experiments will produce clean results (Hilborn and Mangel 1997), as may be observed in certain physical sciences. The geologist T. C. Chamberlain (1897) suggested an alternative approach to science where multiple competing hypotheses are confronted with observation and data. Sorting among alternatives may be accomplished using a variety of scientific tools (experiments, modeling, logical inference). As in geology, it is difficult to conduct critical experiments in the ecological sciences, so observation, inference, good thinking, and models may be used to guide the understanding of the world (Hilborn and Mangel 1997).

Confronting uncertainty, then, is not prescriptive. In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding and used in synthesis for this assessment.

The greatest uncertainties encountered in this assessment involved beaver abundance estimates, beaver fertility and survival, and the effects of human-caused habitat changes on beaver populations (although watershed level and reach level fluvial responses to human influences are fairly well known). Although beaver presence is easy to detect by sign surveys, all field techniques developed to date to census beavers have limited reliability. As a result, knowledge of beaver abundance is essentially lacking for the entire region, other than what can be inferred from qualitative observations and harvest data. This assessment deals with this uncertainty by stating agency population estimates where they exist, identifying the uncertain assumptions on which they are based, and attempting no further analysis of abundance.

The population matrix analyses are based on incomplete knowledge of fertility and survival rates. Several published reports exist on age-specific survival, but most data sources are based on commercial fur harvest records, which are biased by fur prices, trapper effort, trapper selectivity for older age classes, and other factors. In addition, commercially exploited populations may show age class distributions and rates of mortality and fecundity that are significantly altered from non-exploited conditions. We averaged survival and fecundity rates from various reports for analysis in this assessment, and we assumed that the data, although largely from exploited populations, represented the best approximation for all populations, given the absence of other data.

The potential responses of beaver populations to habitat degradation and restoration are highly speculative. No direct measurement data exist on the effects of human-caused habitat alteration or management on beavers. We used information on beaver habitat requirements, and inferences from monitoring reports and personal knowledge of habitat conditions in some areas of Colorado, to develop conservation considerations.

Publication of Assessment on the World Wide Web

To facilitate their use, species conservation assessments are being published on the Region 2 World Wide Web site (http://www.fs.fed.us/r2/projects/scp/). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, Web publication will facilitate updates to and revision of the assessments, which will be accomplished based on protocols established by USFS Region 2.

Peer Review

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose two recognized experts on this or related taxa to provide critical input on the manuscript.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The Nature Conservancy classifies the beaver as N5 (nationwide: demonstrably widespread, abundant, and secure) in the United States and Canada. Within Region 2, this species is ranked S5 (statewide: demonstrably widespread, abundant, and secure) in Kansas, Nebraska, and South Dakota, and S4 (statewide: apparently secure) in Colorado and Wyoming (NatureServe 2005). State wildlife agencies have primary management authority for beavers in all Region 2 states. The beaver is classified as a furbearer by all states in Region 2. Under this designation, beavers are typically managed to provide sustainable sport and commercial fur harvest, and take for damage control is allowed and regulated.

Beavers are designated as a Management Indicator Species (MIS) by the Bighorn National Forest (Wyoming), Routt National Forest (Colorado), Pike–San Isabel National Forests (Colorado/Kansas), San Juan National Forest (Colorado), and Shoshone National Forest (Wyoming). As directed in the 1982 National Forest Management Act, USFS planning unit plans must select MIS and identify monitoring practices for MIS; Environmental Impact Statements accompanying the plans must show the estimated effects of projected management actions on these species. MIS should be chosen to reflect major management issues, for their ability to facilitate evaluation, and with regard to MIS chosen on neighboring planning units where applicable (Hayward et al. 2001). Beavers are selected as MIS to evaluate the effects of plan actions on aquatic and riparian habitats.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

No regional management or conservation plans exist for beavers in Region 2. Each state manages beavers as a furbearer under specific management regulations. In Kansas, Nebraska, and South Dakota, beavers may be harvested without limit by licensed trappers within established harvest seasons, and additional regulations provide for depredation trapping. In Wyoming, unlimited licensed trapping within seasons is allowed in parts of the state. Other areas are designated limited harvest areas, where beaver harvest is more stringently managed by limited permits, season bag limits, and/or season restrictions (Wyoming Game and Fish Department 2004). Limited harvest areas are designated to protect large important beaver populations, mainly at higher elevations on public lands, and include parts of all national forests in Wyoming. In Colorado, voters passed Amendment 14 (CRS 33-6-203) to the state Constitution in 1997; this amendment largely bans lethal methods of trapping and effectively halts sport and commercial harvest. Depredation trapping still is allowed under special regulations.

All Region 2 state wildlife agencies regard current laws and regulations as sufficient to protect beaver populations from overharvest, and they regard enforcement as generally adequate. Beavers are occasionally taken by unauthorized trapping and shooting, but we are not aware of any state agency biologists who believe that such incidences pose a significant conservation threat to beaver populations at regional scales.

Biology and Ecology

Systematics and species description

The American Society of Mammalogists classifies the North American beaver as *Castor canadensis*, Order Rodentia, Family Castoridae (Jenkins and Busher 1979). The family is represented by one genus with two species, *C. canadensis* in North America, and *C. fiber* in EuraAsia. The species are similar in appearance and are distinguished by differences in chromosome number and cranial morphology (Jenkins and Busher 1979).

A lack of extensive taxonomic study has hampered subspecies distinctions within *Castor canadensis* (Osborn 1953). Twenty-four subspecies have been described, but their status and distribution are confused in many parts of the United States, including all Region 2 states, by reintroductions of beavers obtained from elsewhere in North America (Wilson and Ruff 1999). The Colorado subspecies is *C. c. concisor* (Fitzgerald et al. 1994). In Wyoming, *C. c. concisor* is the dominant subspecies, with populations of *C. c. taylori* occupying the Snake River drainage (Osborn 1953). *Castor c. carolinensis* historically occurred in Kansas before its extirpation, and it has been replaced by *C. c. missouriensis* (Bee et al. 1981), which occurs throughout the Great Plains states, including South Dakota and Nebraska. Originally, the subspecies were presumably segregated by major watersheds.

The beaver is North America's largest rodent, weighing between 11 and 32 kg. Beavers have a total body length of 64 to 120 cm, of which 20 to 35 cm is the wide, dorsally flattened, scaly tail (Jenkins and Busher 1979, Deems and Pursley 1983). Average body length and weight are reported in the literature for the following Region 2 states: 94 to 121 cm and 14 to 27 kg for Kansas (Bee et al. 1981), 64 to 76 cm and 14 to 28 kg for South Dakota (Higgins et al. 2000), and 85 to 120 cm and 16 to 32 kg for Colorado (Fitzgerald et al. 1994). Body size increases with increasing latitude (Deems and Pursley 1983) and varies with longitude, with mid-continent beavers attaining the largest sizes (Baker and Hill 2003). Body weight and tail size (length x width) are useful criteria for placing beavers into age classes (Townsend 1953, Patric and Webb 1960, Easter-Pilcher 1990).

The body form is thick and heavily muscled, broadest just anterior to the hips and tapering gradually toward the nose, with shorter legs in the front than in the rear (Novak 1987, Baker and Hill 2003). The large head is supported by a short, thick neck almost continuous with the shoulders; small round ears and small eyes are located high on the head (Baker and Hill 2003). The broad tail is used for communication and fat storage, and as a heat exchange organ (Novak 1987). Beavers are sexually monomorphic in appearance and size; the sexes can be distinguished by the swollen nipples of lactating females (Novak 1987) and by the color of their anal gland secretion (Schulte et al. 1995). Pelage is molted annually during the summer (Novak 1987), and it ranges in color from blackish to dark brown and chestnut (Fitzgerald et al. 1994), with the most common color being reddish brown (Jenkins and Busher 1979). Long, coarse, shiny guard hairs function to repel dirt and water, and cover the dense underfur (Novak 1987). The limbs each have five digits. The small forefeet are clawed for digging and are extremely dexterous for manipulating food, carrying building materials, and transporting young. The large hindfeet are webbed between the toes for swimming, with the second digit split like a comb for grooming (Baker and Hill 2003).

Beavers have 20 teeth, including long, chisel-shaped incisors for cutting. The incisors grow continuously, and have a hard, orange enamel mineralized with iron and calcium (Wilson and Ruff 1999). The underlying soft white dentin wears faster to maintain a sharp cutting edge (Novak 1987). A massive skull and mandible support the large muscles needed to cut woody vegetation (Baker and Hill 2003).

Beavers have well-developed senses of hearing and smell but weak eyesight, since they may spend 3 to 8 months out of the year in darkness under snow and ice in higher latitudes and mountains (Novak 1987). Two sets of paired anterior glands produce secretions for intraspecific scent communication. Lipid-rich anal gland secretions also add water-repellency to the pelage (Novak 1987). Castor gland secretions mix with urine to form castoreum (Novak 1987), important for territorial communication (Aleksiuk 1968) and advertising mating status (Butler and Butler 1979 in Novak 1987).

The beaver is highly specialized behaviorally and physiologically for its semi-aquatic lifestyle. On land, the beaver is clumsy and hump-backed, but in water, it is an excellent swimmer with a streamlined body, propelling itself with its webbed hindfeet and using the tail as a rudder (Novak 1987). On land, the tail functions to maintain balance, especially when walking on hind legs while carrying building materials with the forefeet (Wilson and Ruff 1999). Underwater, nictitating membranes protect the eyes, and valves automatically constrict to close the ears and nose (Jenkins and Busher 1979). The dense underfur creates an insulating air layer that helps to retain body heat (Scholander et al. 1950 in Novak 1987).

Beavers normally dive between 1 to 2 minutes, but they may stay underwater up to 15 minutes (Irving and Orr 1935 in Jenkins and Busher 1979). Physiological adaptations for diving include up to 75 percent lung exchange capacity, a high tolerance for elevated blood carbon dioxide levels (Rue 1964 in Novak 1987), and a reduction in heart rate up to 79 percent (McKean 1982 in Novak 1987). Fur-lined lips close behind the incisors and allow the beaver to carry branches in its mouth while preventing water from entering the lungs (Wilson and Ruff 1999). An elevated tongue and intranarial epiglottis also prevent the beaver from taking water into the larynx and trachea (Coles 1970 in Novak 1987). Physiological adaptations for winter survival include fat storage in the tail, reduced activity, and lowered body temperature (Wilson and Ruff 1999).

Distribution and abundance

The North American beaver occurs throughout most of Alaska, Canada, the continental United States, and in portions of northern Mexico (**Figure 1**). Beavers are absent from the tundra of northern Alaska and Canada, parts of the Midwest, much of South Carolina, and peninsular Florida (Novak 1987, Baker and Hill 2003). In arid regions of the southwestern United States, beavers only occur along larger streams and rivers. The North American beaver has been successfully introduced to southern South America and to Europe, where *Castor canadensis* now outnumbers the native *C. fiber* in some areas (Härkönen 1999).

The present range of the beaver covers most of its historic range (Baker and Hill 2003), with a current North American population thought to number between 6 and 12 million (Naiman et al. 1988, Ringelman 1991). This represents a small fraction of the estimated 60 to 400 million beavers that occupied North America before European settlement (Crowe 1986, Ringelman 1991). This decline from historic levels is attributed to the impact of a mostly unregulated fur trade in the 18th and 19th centuries that decimated populations throughout most of the beaver's range by 1900 (Novak 1987, Wilson and Ruff 1999, Baker and Hill 2003). Commercial beaver harvest in North America began in the 1600's in the Northeast (Wilson and Ruff 1999), and spurred by European fashion trends, it escalated to high levels by the early 1700's. From the 1700's to about 1850, the fur trade (primarily beaver) was the dominant economic activity in Canada and the United States west of the settlement frontier. In fact, most exploration of the North American West was undertaken in search of new furbearer populations and fur transportation routes (Rutherford 1964, Deems and Pursley 1983). Exploitation of beavers increased with the invention of the steel leghold trap around 1825 (Polechla 1989) and increased reliance of Native Americans on beavers for their economic value (Henderson 1960, Wessels 2001). By the end of the 1800's, beavers were locally extirpated from many watersheds in Region 2 states, with remaining populations severely reduced (Deems and Pursley 1983, Larson and Gunson 1983).

Conservation efforts began in the early 1900's, and by the 1950's all Region 2 states (as in other parts of North America and Canada) were monitoring harvest and enforcing trapping regulations. State

Figure 1. Distribution of the North American beaver (from Baker and Hill 2003).

and provincial efforts to manage beaver populations sustainably have led to recovery and maintenance of stable populations in many parts of the beaver's range (Novak 1987). Current populations in all Region 2 states are derived from remnant historical populations or natural re-colonization. These populations have been supplemented by natural increase, live trapping and relocation efforts, and introductions from other states (Larson and Gunson 1983).

In Colorado, the commercial fur trade severely depleted beavers in most areas by about 1850 (Rutherford 1964). Although the heyday of the beaver trade was over, unchecked exploitation continued to depress populations, with a low point probably reached between 1890 and 1900. With state protection from harvest after about 1900, populations began a steady recovery. From about 1900 to 1960, Colorado allowed only a regulated harvest for control of damage to private property, and nearly all trapping occurred on private lands. In areas where suitable habitat remained, particularly on public lands, many beaver populations reached habitat carrying capacity by the 1950's (Retzer et al. 1956, Rutherford 1964). Beginning in 1956, Colorado allowed beaver trapping for commercial harvest and damage control. By the 1960's, beavers were again common in all major watersheds of Colorado (Rutherford 1964), but they remained absent or reduced in areas where urban and agricultural development had destroyed beaver habitat. From 1956 to 1995, annual take varied from about 5,000 to 20,000 beavers. In 1996, a citizen referendum amended the state constitution to prohibit lethal trapping in Colorado, effectively eliminating commercial and sport trapping. The Colorado Division of Wildlife has no data on beaver population size or distribution in Colorado, but based on anecdotal information, they believe that beavers are fairly common throughout the state and increasing in some areas (Colorado Division of Wildlife 2004).

In Kansas, an estimated historic population of 50,000 beavers was drastically reduced by the late 1800's (Henderson 1960). Baker (1889) reported the beaver's rapid disappearance from western Kansas, and Cockrum (1952 in Henderson 1960) described an 1899-1900 expedition in northern Kansas that found only one beaver colony. Beaver protection in Kansas began in 1927 with a law prohibiting the destruction of beaver dens and dams, and requiring licenses for fur dealers (Henderson 1960). In 1937, the state population was estimated to be 1,500 beavers (Wall 1939 in Henderson 1960). The state wildlife agency transplanted beavers to several sites between 1930 and 1950, increasing beaver abundance and distribution in the state. By 1959, beavers had established permanent populations in 100 of 105 counties, and an estimated 23,000 beavers occurred in all five major river systems and many man-made reservoirs (Henderson 1960). Beavers are now widespread in suitable habitats in Kansas (Bee et al. 1981), occupying the larger rivers typical of eastern Kansas, as well as smaller streams of the western part of the state. They are generally most abundant in the larger river systems (Henderson 1960).

In Nebraska, depletions of beaver by the commercial fur trade prompted the state legislature to grant the species complete protection in 1907. Nebraska populations may not have been decimated as badly as in other Region 2 states, as M. H. Swenk's unpublished notes from 1910 to 1930 mention beavers as relatively abundant, especially along major rivers. Beaver damage claims by farmers provided further evidence of beaver occupation (Jones 1964). Today in Nebraska, beavers are widespread statewide in suitable habitat. The Nebraska Game and Parks Commission has no direct data on beaver population numbers or distribution, but based on anecdotal information, they believe that beavers are common and very widespread in the state. The Nebraska Game and Parks Commission monitors annual beaver harvest by trapper and fur buyer surveys, and estimated the beaver harvest in 2002-2003 at about 15,000, near the 5-year average of 18,000 (Nebraska Game and Parks Commission, unpublished data).

No historic population estimates are available for South Dakota, but beaver populations have experienced the same decline and recovery as in other Region 2 states. Beavers now occur in suitable habitat in all South Dakota counties, with the greatest number of records in the eastern counties (Higgens et al. 2000). Most habitat occurs in riverine wetlands and riparian areas, but beavers sometimes occupy potholes and other marsh wetlands. The 2003 population was estimated at about 59,300 beavers, and fur harvest is monitored by a survey of licensed fur buyers, who bought an estimated 3,238 pelts during the 1986-87 season (Huxoll 2003).

In Wyoming, fur trapping became active around 1820, and beavers were nearly extirpated from much of the state by 1860 (Olson and Hubert 1994). Anecdotal reports from Yellowstone National Park suggest that beavers were common as late as the 1870's and 1880's, declined by 1900, then largely recovered by the 1930's (Kay 1994). Commercial overharvest was probably the most important factor in the statewide decline of the 1800's, but riparian habitat degradation by overgrazing livestock (and wild ungulates in Yellowstone National Park) was also probably important (McKinstry et al. 2001). An 1899 law gave beavers complete protection from harvest in Wyoming (Collins 1993 in Olson and Hubert 1994), and reintroductions further aided recovery. By 1958, populations were sufficiently recovered to reclassify the beaver to furbearer (Olson and Hubert 1994), allowing regulated harvest and population management. Beavers now occur throughout Wyoming wherever suitable habitat exists (Crowe 1986), but riparian habitat degradation, caused primarily by livestock grazing, has reduced available habitat (McKinstry et al. 2001). McKinstry and Anderson (1999) used data from a survey of Wyoming landowners and public land managers to estimate density at 2.8 beavers per kilometer of stream in occupied habitat, and 1.2 beavers per kilometer of stream statewide. McKinstry et al. (2001) estimated that beavers have been extirpated from about 25 percent of all Wyoming streams where they presumably occurred historically, and in some occupied streams, beaver populations are low enough that beavers can be considered "ecologically absent" (McKinstry and Anderson 2002). The Bighorn National Forest Draft Forest Plan Revision (2004) states that beavers are distributed forest-wide although populations have been reduced from historic levels. The Shoshone National Forest Fiscal Year 2002 Forest Plan Monitoring and Evaluation Report states that the Forest in general does not provide good beaver habitat because of steep and narrow drainages, unstable volcanic substrates, and limited deciduous food supplies.

Population trend

No quantitative data exist on beaver abundance or population trend for any Region 2 state. Based on indirect evidence, beaver populations at a broad scale throughout Region 2 are thought to be stable or increasing. However, it should be noted that much of the indirect evidence is from harvest trends, which are strongly influenced by fur prices and other factors besides beaver abundance, and nuisance complaints, which are influenced by changes in human settlement patterns. With these caveats in mind, beaver populations in Kansas are considered stable, based on harvest surveys and increases in nuisance complaints (Peek personal communication 2004). In Nebraska, statewide beaver populations are considered stable to increasing based on similar indirect evidence. However, in the prairie ecosystems of western Nebraska, local populations are thought to have been depressed by drought from 2000 to 2004 (Hack personal communication 2004). In South Dakota, beaver populations appear to be increasing statewide, based on county wildlife surveys (Huxoll 2003). In Colorado, no statewide harvest surveys or other evidence of beaver abundance have been maintained since lethal trapping was effectively ended in 1996 (Apker personal communication 2004). Anecdotal observations by Colorado Division of Wildlife personnel of beaver distribution and damage complaints suggest a generally stable population, with increases in some areas. The Wyoming Game and Fish Department reports the long-term population trend is stable (Rothwell personal communication 2004). McKinstry and Anderson (1999) believed that Wyoming beaver populations were stable or increasing, based on their survey of Wyoming landowners and public land managers. They also reported that decreased trapping pressure from a depressed fur market and greater public tolerance of beaver presence might be contributing to beaver population increases on private land. Still, some public land managers report decreasing populations, citing degraded habitat quality as the cause 60 percent of the time.

Activity and movements

Where stream size and adequate woody material allow, beavers construct dams to impound water (Baker and Hill 2003), a unique behavior that profoundly influences their habitat and community ecology. Beavers impound water to expand their habitat and accessible foraging territory, to increase their aquatic food supply, to protect themselves from predators, and to provide sufficient water depth for over-winter survival in cold regions (Easter-Pilcher 1987, Naiman et al. 1988).

Beavers shelter in constructed lodges and bank dens for resting, breeding, escape from predators, and thermoregulation (Jenkins and Busher 1979). In ponds and shallow lakes, they construct a lodge, a dome-shaped structure made of woody stems held together with mud (Allen 1983). An underwater entrance leads to a feeding chamber, and a higher and drier chamber is used for sleeping and rearing kits (Baker and Hill 2003). On larger rivers and in deep lakes, beavers sometimes build lodges on shore, with an underwater entrance (Henderson 1960). Beavers also dig bank dens on the shore of rivers, streams, ponds, and lakes. They may use both bank dens and lodges, or only bank dens. Bank dens have an underwater entrance and one or more narrow openings to the ground surface for ventilation (Baker and Hill 2003). Lodges and dens provide a year-round thermoneutral zone for beavers (Buech et al. 1989 in McKinstry et al. 1997), important for winter survival in colder regions. In summer, other dens may be used as kits are being born, yearlings expand their range, or the colony extends its territory. By fall, additional dwellings are abandoned, and the entire colony returns to the main lodge (Hay 1955), where huddling behavior helps to conserve body heat.

Building and maintenance of the dam and lodge are stimulated primarily by auditory cues and changing water levels. Rising water level triggers lodge maintenance. Falling water levels or the sound of running water stimulate beavers to patch dams with small repairs, while a stronger stimulus such as the sound of rushing water stimulates dam building or major repairs (Wilsson 1971 in Jenkins and Busher 1979). Beavers begin dam construction by embedding materials in the streambed, then weaving together saplings, small trees, and logs, sometimes peeled of their bark (Novak 1987, Wilson and Ruff 1999). Woody material is placed parallel to the stream current, and mud and stones plastered on the upstream side help to make the dam watertight (Novak 1987). Dam construction occurs during high water periods such as spring runoff, or in the fall to prepare for winter. Beavers usually build one “home” dam to create a pond for the main lodge. Secondary dams may also be built depending on food availability, soil type, and terrain (Rutherford 1964). Sometimes these dams are built at different levels, resulting in a “lock” system to control water at each level. Secondary dams allow beaver to transport food and materials to the home pond over greater distances while minimizing travel over dry land (Rutherford 1964). Beavers often construct extensive canal systems in shallow ponds or wetlands to aid in the transport of cut wood (Novak 1987).

In northern latitudes and higher elevations in Region 2, beavers construct a food cache near the den or lodge to store woody vegetation for winter food. Food caching is infrequent south of 38° N latitude (Hill 1982), and irregular in lower elevation streams in the Colorado mountains (Yeager and Rutherford 1957). Construction usually begins after the first heavy frost (Novak 1987), and begins with a floating raft of cuttings under which twigs and small branches to be used for food are placed (Fitzgerald et al. 1994).

Beavers live in colonies, which can be defined as a group of beavers occupying in common a pond, ponds, or a stretch of stream, utilizing the same food cache, and maintaining communal dams where habitat allows (Hay 1955). A family colony usually consists of an adult breeding pair, their young of the year (kits), and the previous year's offspring (yearlings), and it may occasionally include one or two non-breeding subadults (Rutherford 1964, Novak 1987). Less commonly, pair colonies contain an adult pair with no offspring, and single "colonies" contain an un-paired non-migratory adult occupying and defending a territory. Percentages of colony types from various populations have been reported ranging from 59 to 66 percent family colonies, 20 to 24 percent pair colonies, and 14 to 17 percent single colonies (Payne 1984a). Family colony size typically ranges from three to eight beavers, with larger colonies occurring in the middle parts of the beaver's range (Novak 1987). In Colorado, Rutherford (1964) found an average 5.1 beavers per colony in aspen habitat and 4.5 beavers per colony in willow habitat. Peterson and Payne (1986) observed an average 5.6 beavers per family colony, and 3.7 beavers for all colony types in Wisconsin. Bhat et al. (1993) estimated an average of 4.8 beavers per colony in New York. When calculating population parameters from colony sampling data, an average of five beavers per colony is often assumed (i.e., Hay 1955, Henderson 1960, Fitzgerald et al. 1994).

Most beaver activity occurs near the lodge or pond, the colony's main territory (Rutherford 1964, Aleksiuk 1968). In a typical family colony, the adult female dominates most activities including initiating lodge construction, maintaining the lodge and dam, and building the food cache. The entire family (except young kits confined to the den) helps to defend the colony and conduct all activities (Fitzgerald et al. 1994). Activities outside of the lodge, such as building, cutting, and territory defense, are conducted independently. Beavers groom themselves and engage in mutual grooming, but this activity is not known to promote social bonds (Novak 1987).

Beavers are primarily nocturnal and crepuscular (Novak 1987, Baker and Hill 2003), but they may be active during any part of the day. In summer, beavers begin activity earlier in the day and are active for longer periods (11 to 13 hours) compared to winter (e.g., 7.5 hours in November) (Novak 1987). In winter, beavers may display a circadian rhythm of 26 to 28 hours when living under pond ice in the shelter of the lodge (Wilson and Ruff 1999).

Territory size depends on habitat factors such as valley width, stream gradient, food availability (Rutherford 1964), and water, as well as the size of the colony (Brenner 1967 in Allen 1983). Territory size ranges from 0.4 to 8 ha. The average territory size in Colorado ranges from 1.6 to 3.2 ha (Fitzgerald et al. 1994). Although territory boundaries are not precisely defined (Novak 1987), colony boundaries may be determined by factors such as steep topography, winter food supply, or territorial defense by adjacent colonies (Rutherford 1964, Allen 1983).

Beavers mark their territories with scent mounds constructed of mud and vegetation scented with deposits of castoreum (Baker and Hill 2003). Scent mounds are most often placed at the water's edge at territory boundaries and in high activity areas near dams, lodges, and trails (Aleksiuk 1968, Novak 1987). Peak scent-marking activity begins after spring ice break-up and remains high through May to mid-June, coinciding with the period of litter birth and juvenile dispersal (Novak 1987). Scent mounds advertise the sex and age status of beavers in a colony. For example, if a dispersing beaver detects an absence of scent from an adult of the opposite sex, it may join the colony and become part of a new breeding pair (Butler and Butler 1979 in Novak 1987). The number of scent mounds has been reported as typically 2 to 7 per colony (Nowak 1987), but may reach over 100 (Schulte personal communication 2006). The use of scent mounds is density-dependent. Müller-Schwarze and Heckman (1980 in Novak 1987) found that scent mounds were used less frequently or not at all when the nearest colony was more than 500 m away. In Montana, Easter-Pilcher (1987) found that scent mounds were numerous where beaver colonies were close together, but absent at other isolated colonies. Territorial behavior imposes limits on the size of local beaver populations and represents an important limit on beaver utilization of food resources and overall habitat impact (Aleksiuk 1968, Easter-Pilcher 1987, Baker and Hill 2003).

Beavers communicate with each other by various movements and vocalizations (Baker and Hill 2003). Tail slapping, in which a beaver loudly smacks its tail on the water surface, functions to warn other beavers of danger, to scare enemies, or to elicit a response from other beavers (Novak 1987). Kits vocalize most often, whining or mewing to beg for food or to initiate grooming and play (Novak 1987). Antagonistic interactions consist of hissing and growling, and movements such as tail quivering, biting, and lunging (Novak 1987). Brady and Svendson (1981 in Novak 1987) observed antagonism mainly in the spring, when yearlings begged adults for food. Antagonistic behavior may also occur during territorial interactions, and toward juvenile beavers reluctant to disperse from the colony.

Bergerud and Miller (1977) described major types of beaver movements as movement of an entire colony between ponds within a territory, short-term wandering of yearlings, natal dispersal of beavers to establish new colonies, and miscellaneous adult movements, often following the loss of a mate. Natal dispersal, movement from the colony of birth, typically occurs during the second summer after birth (Allen 1983, Novak 1987) and often coincides with the birth of kits. Dispersal date is variable due to local habitat and climate conditions, but it generally occurs from April to May or early June (Van Deelen and Pletscher 1996, Sun et al. 2000). Dispersing when water levels are high allows beavers to reach areas not accessible during low water periods, and presumably decreases mortality rate through predator avoidance. In landscapes with surrounding high population densities, young beavers may disperse at a later age (Van Deelen and Pletscher 1996, Schulte and Müller-Schwarze 1999); this is a common characteristic of "nuisance" beaver populations (Peterson and Payne 1986). Data suggest that delayed dispersers have greater success establishing themselves in neighboring colonies (Sun et al. 2000).

Secondary dispersal of adult beavers may be caused by food shortages, flooding, insufficient stream flow, searching for a new mate, or human disturbance (Leege 1968). Sun et al. (2000) reported that adult secondary dispersal accounted for 39 percent of all movements in a New York population, and that males are more likely to make secondary dispersals than females. Leege (1968) observed that about 33 percent of all adults in a southeastern Idaho population had moved at least 1.6 km after one year.

Dispersal distance varies depending on age, sex, habitat, and other factors. Average natal dispersal distances for 2-year-old beavers have been reported from 0.8 to 20.8 km (Novak 1987). Average dispersal distances from various studies include 3.5 km for males and 10.2 km for females in New York (Sun et al. 2000), 18 km for beavers in Quebec (Courcelles and Nault 1983 in McKinstry and Anderson 2002), and up to 18 km for beavers in southeastern Idaho (Leege 1968). Van Deelen and Pletscher (1996) and Hibbard (1958) found that dispersal distance did not correlate with date of dispersal or time taken to locate a settlement site, and that the probability of dispersal and dispersal distance were independent of gender. Dispersal occurs more often in the downstream direction, which is less costly energetically than travel upstream (Sun et al. 2000). Two-year old beavers in Montana moved an average maximum of 3.0 to 4.7 km upstream and 4.7 to 7.0 km downstream (Van Deelen and Pletscher 1996). It is unclear if transplanted beavers exhibit dispersal patterns different from those of naturally dispersing beavers. Reported average distances traveled by transplanted beavers include 17.0 km in Colorado (Denney 1952 in Hibbard 1958), 14.6 km in North Dakota (Hibbard 1958), 7.4 km in Wisconsin (Knudsen and Hale 1965 in McKinstry and Anderson 2002), and 11.2 km in Maine (Hill 1982). In Wyoming, 51 percent of beavers (58 total) transplanted by McKinstry and Anderson (2002) emigrated over 10 km from their release sites within 180 days.

Dispersers may take several months to locate and settle into suitable habitat (Sun et al. 2000). Van Deelen and Pletscher (1996) observed beavers in Montana settling into a new territory from two to 181 days after beginning dispersal; the latest settlement date recorded was in mid-November. Dispersal success depends on habitat suitability and the extent of existing occupation of potential sites. Dispersing beavers are less successful in establishing new territories if suitable habitat is patchy (Fryxell 2001).

Habitat

Beavers occupy aquatic habitats in a wide variety of ecosystems throughout their North American range, including desert, semiarid shrubland, montane and subalpine forest, and human-altered agricultural lands, rangelands, and urban areas. Their ability to modify habitat to meet their needs makes them extraordinarily adaptable to diverse landscapes (Gurnell 1998). The beaver's primary habitat requirement is a permanent body of water with an adequate and accessible food supply (Allen 1983, Novak 1987, Gurnell 1998). Although beavers are widely distributed in Region 2, their requirement for stable, permanent water limits them to a fraction of the landscape. Rutherford (1964) estimated that beaver habitat in the Colorado mountains occupies about 2.5 percent of the total watershed area, based on an assumption that beavers forage up to 100 m from suitable streams.

At lower elevations of Region 2, beaver habitat is often characterized by riparian forests dominated by cottonwood and willow along river systems on the relatively flat plains or streams in foothills drainages. This habitat is typical of the Great Plains in Kansas, Nebraska, South Dakota, and eastern Colorado and Wyoming (Rutherford 1964, Bee et al. 1981, Welch et al. 1993), and it occurs in the semiarid steppes and valleys of western Colorado and Wyoming. Most plains river bottom habitat occurs on privately owned agricultural lands and rangelands, where beaver activity is often considered to conflict with human land uses (Rutherford 1964, Welch et al. 1993).

At higher elevations in Region 2, beaver habitat is typically in streams with low to moderate gradient (usually less than 12 percent) in mountain valleys and basins. These stream habitats are commonly associated with montane riparian vegetation communities dominated by cottonwood, aspen, alder, or willow (Allen 1983, Novak 1987, Olson and Hubert 1994). These montane systems comprise the primary beaver habitat on National Forest System lands of Colorado and Wyoming and the Black Hills National Forest of South Dakota.

Beavers in Region 2 also occupy natural lakes, prairie potholes, artificial reservoirs and ponds, and irrigation canals and ditches (Robel and Fox 1993, Welch et al. 1993). Large lakes (over 8 ha in size) must have a shoreline with sheltered coves or bays that protect colonies from strong wind and waves (Slough and Sadleir 1977, Allen 1983). Lower quality habitat includes lakes and streams with rocky shorelines, flood-prone areas, fast-moving water, or widely fluctuating water levels, and drought-vulnerable wetlands such as prairie potholes (Allen 1983, Novak 1987). Although beavers sometimes colonize these habitats, these sites are typically unproductive and likely to be population sinks. Beavers tolerate human presence and commonly occur near human developments as long as persecution or habitat alternation is not severe (Slough and Sadleir 1977).

The upper elevation limit for beaver occupation is determined by the distribution and abundance of woody vegetation in or near riparian areas (Retzer et al. 1956), which is limited by a short growing season at extreme altitudes (Rutherford 1964). Despite these limitations, beavers frequently occupy high altitude willow fields above 11,000 feet (Retzer et al. 1956), as long as they can impound a sufficient depth of water along suitable streams (Slough and Sadleir 1977). The availability of woody vegetation is assumed to be a limiting habitat factor for beaver populations that depend on a stored food cache for winter survival (Allen 1983).

Beaver habitat characteristics vary widely across their range, but in Region 2 where most beavers occupy rivers and streams, the most important habitat factors are a stable, permanent water supply; the distribution and abundance of suitable woody plant species; and stream characteristics including gradient, channel features, and valley width (Allen 1983, Easter-Pilcher 1987, Baker and Hill 2003).

The beaver's primary habitat requirement is a stable, permanent body of water that provides concealment and escape routes for beavers and protects entrances to the lodge or bank den (Allen 1983). Streams with swift water (Olson and Hubert 1994) or highly fluctuating flows are less suitable or unusable (Martin 1977, Gurnell 1998). Pond water depth must be sufficient to cover lodges or bank dens, and to allow beavers to move freely under ice to access the food cache (Yeager and Rutherford 1957, Slough and Sadleir 1977). Beavers are highly adept at modifying water characteristics by damming, which improves the seasonal reliability of water and provides pools of sufficient depth. Canals constructed by beavers also extend the reach of water bodies to access food plants.

Woody deciduous vegetation is essential to beavers for food, building materials, and cover when traveling on land (Slough and Sadleir 1977, Novak 1987). Ringelman (1991) estimated that a colony of six beavers can be supported by 1.6 ha of aspen, 4.9 ha of willow, or an intermediate combination of the two. The beaver Habitat Suitability Index (HSI) model (Allen 1983) assumes optimum food availability where forest canopy cover is 40 to 60 percent, with a medium density of preferred food species less than 6 inches in diameter. Food is presumed to be less accessible where canopy cover exceeds 60 percent because cut trees may get caught in the canopy rather than fall to the ground. Food plants are essentially woody riparian species whose abundance depends on factors that influence riparian community distribution and structure. Beaver food abundance thus depends on the stability of surface and subsurface water, soil, climate, elevation, aspect, and community successional stage, which can be strongly influenced by beaver feeding and construction (Rutherford 1964, Slough and Sadleir 1977). In high altitude areas of the Rocky Mountains, slow plant growth and a short growing season limit beaver food production, contributing to less productive beaver populations at increasing altitudes (Yeager and Rutherford 1957, Rutherford 1964).

Channel features important for beaver habitat include stream beds and banks of stable soil with some gravel or cobble; streams over bedrock or coarse rocky beds do not provide suitable places to anchor building materials (Gurnell 1998). Shale is often geologically unstable and limits beaver habitat where streams are highly erosive (Yeager and Rutherford 1957). Bank-dwelling beavers can be limited by rocky substrates or steep, highly erosive banks (Olson and Hubert 1994). In mountainous regions, streams with less than 6 percent gradient and slow-moving flows are optimal for dam-building beavers, and streams with gradients exceeding 13 percent are unsuitable due to fast flows, high flood potential, and often unpredictable water supply (Retzer et al. 1956, Allen 1983). Low gradient valley drainages are usually broader, providing not only optimal hydrological regimes, but also more floodplain area for the growth of woody vegetation (Retzer et al. 1956). A low gradient, high sinuosity, and wide, well-vegetated floodplain allows seasonal floodwaters to disperse, and dissipate floodwater energy, reducing damage to beaver structures. Broad valleys also allow larger pond areas because small increases in dam height result in large increases in pond surface area (Gurnell 1998). At lower elevations where streams and rivers have low gradients, beavers are able to occupy most drainages as long as adequate food and security exist. Bank-dwelling beavers that do not build dams may occupy higher order streams with high flow volumes (Parker et al. 1985, Naiman et al. 1988). High gradient or entrenched streams, which are typical in canyons and narrow mountain valleys, are poorly suited for beavers, due to the limited area for food growth and the high stream power (Retzer et al. 1956).

Mathematical models of beaver habitat have been developed to test hypotheses and to make predictions for beaver conservation and management (many reviewed by Baker and Hill 2003). A discriminant-function model developed from vegetation and stream characteristics in northwestern Montana identified the following critical variables for winter colony site location: water depth, horizontal distance between high and low water marks, and availability of willow (Easter-Pilcher 1987). Slough and Sadleir (1977) developed a land-classification system for beavers in Ontario based on regression analysis of sample data on beaver colony density and associated habitat characteristics. Howard and Larson (1985) predicted beaver colony density in Massachusetts based on statistical models of habitat variables. The most applicable model for Region 2 is the general HSI model for beaver, developed from literature review and expert opinion by Allen (1983) and widely used to quantify potential impacts from development projects and to plan and measure mitigation and restoration efforts. The HSI model rates habitat quality based on nine variables: canopy cover, height, stem diameter, species of trees and shrubs, stream gradient, water level fluctuation, and the ratio of shoreline length to lake area. The HSI model specifies a minimum habitat area of 0.8 km of stream or 1.3 km^2 of lake or marsh to be suitable for beavers.

Food habits

Beavers are central place foragers, gathering food and carrying it to a central location in the territory to be consumed (McGinley and Whitham 1985). Most trees are cut within 100 m of the water's edge (Rutherford 1964, Allen 1983). The farthest cutting is usually done on steep slopes, which make branches and logs easier to transport over long distances, and increases the beaver's chance of escaping from predators (Novak 1987). Of all trees cut, an estimated 10 to 64 percent are "wasted" (e.g., not utilized for food or building). Most losses are from larger diameter trees because beavers eat mostly the smaller branches and twigs from the top and discard the rest (Fitzgerald et al. 1994). At increasing distance from water, beavers select fewer but larger trees and are more species-selective (Gallant et al. 2004), with the effect greatest in high-quality habitats.

Beavers are herbivores, primarily subsisting year round on the inner bark, twigs, leaves, and buds of deciduous woody plants (Wilson and Ruff 1999, Baker and Hill 2003), but they also eat many herbaceous and aquatic plant species, especially in summer (Allen 1983). Although beavers utilize a wide range of woody and herbaceous plant species (with diet diversity increasing southward in the beaver's range) (Novak 1987), most of their food is taken from a small number of preferred species (Jenkins and Busher 1979). Throughout their range, beavers prefer species from the willow family (Salicaceae), especially aspen (*Populus tremuloides*) where it is available (Retzer et al. 1956, Rutherford 1964, Novak 1987, Basey 1999). The bark of these species is high in protein and easily digestible (Wessels 2001). Aspen is a higher quality beaver food than willow (*Salix* spp.) (Rutherford 1964), but once aspen has been depleted or where willow is the dominant deciduous woody species, beavers feed primarily on willows (Retzer et al. 1956). Nolet et al. (1994) found that beavers in willow-dominated habitat in the Netherlands fed mostly on willow but selected uncommon non-willow species in greater proportion than their availability, suggesting that willows alone may not provide sufficient trace nutrients such as sodium or potassium. In plains riverbottom habitat, cottonwood (*Populus* spp.) is the preferred food species, supplemented by willow (Bee et al. 1981, Welch et al. 1993). In northwestern Montana, Easter-Pilcher (1987) found that beavers preferred small willows, except where cottonwood was abundant, and preferred stem diameters less than 5 cm.

Beavers in Region 2 also eat other deciduous species including alder (*Alnus* spp.), birch (*Betula* spp.), and currant (*Ribes* spp.). Coniferous species such as pines, spruces, and firs are sometimes consumed but have lower nutritional value to beavers than deciduous species (Novak 1987). In Colorado, Yeager and Rutherford (1957) noted that cutting of conifers usually indicated the exhaustion of preferred food species. Coniferous species and alder are often used for building or for capping the food cache rather than for food (Novak 1987). Beavers have consumed tamarisk (*Tamarix* spp.) in Arizona (Hensley and Fox 1948) and utilize it to some degree in Colorado and Wyoming where it has invaded lower elevation river systems (Olson and Hubert 1994).

Food preferences vary with season due to changes in the availability and nutritional value of food species (Jenkins 1979). Aleksiuk (1970) reported that beavers in Alaska ate the leaves and growing stem tips of willow from July to August, and during the rest of the year, they ate bark from willow (76 percent), aspen (14 percent), and alder (10 percent). In Region 2, beavers may supplement woody species in their summer diet by also consuming herbaceous and aquatic plants such as grasses, sedges (*Carex* spp.), water lily (*Elodea* spp.), cattail (*Typha* spp.), pondweed (*Potamogeton* spp.), duckweed (*Lemma* spp.), duck potato (*Sagittaria* spp.), and horsetail (*Equisetum* spp.) (Rutherford 1964, Allen 1983, Novak 1987). Where available, roots and rhizomes of aquatic plants may provide an important supplement to the food cache in winter (Allen 1983). Beavers inhabiting agricultural lands sometimes consume crops such as corn and soybeans (Ringelman 1991).

In southern or low altitude portions of their range, beavers cut trees and shrubs for food throughout the year, but they cut more in late fall after green herbaceous vegetation has desiccated, and in early spring before new leaves have emerged (Allen 1983). In winter, especially in northern and mountainous portions of their range, beavers depend on a stored food cache of woody vegetation beneath pond ice (Novak 1987). The quality of winter food is important for breeding success because gestation occurs during the period of ice-over and kits are born in early spring before much growing vegetation is available (Easter-Pilcher 1987, Wilson and Ruff 1999).

Beavers select the most nutritious parts of woody plants, and physiological adaptations enable them to digest woody vegetation (Novak 1987, Baker and Hill 2003). Commensal microbes in the caecum enable beavers to digest about 33 percent of consumed cellulose, similar to ruminant mammals (Currier et al. 1960). A cardiogastric gland that increases digestive fluids in the stomach further aids digestion of woody material. Bacterial metabolism in the caecum produces a soft green fecal material that beavers deposit on land and consume to obtain nutrients made available by the bacteria (Baker and Hill 2003).

Vegetation consumption can range from 0.5 to 2.5 kg per day (Novak 1987). Belovsky (1984 in Baker and Cade 1995) estimated beaver summer food consumption at 551 g dry weight per day of hardwood leaves, bark and twigs, and 69 g per day of herbaceous aquatic plants.

Breeding biology

Beavers are monogamous (Deems and Pursley 1983, Wilson and Ruff 1999), breeding from January to February throughout their range, and during the period of confinement to the winter lodge in northern parts of their range (Rutherford 1964). Beavers mate underwater (Novak 1987), and the female produces a vaginal plug two days later that prevents further copulation (Doboszynska and Zorowski 1983). Gestation lasts between 100 and 110 days (Deems and Pursley 1983), and females give birth in the main lodge or den chamber. Beavers produce one litter (averaging three or four kits) per year (Jenkins and Busher 1979, Novak 1987, Baker and Hill 2003), with the kits born from late April to June depending on latitude and elevation (Bee et al. 1981, Wilson and Ruff 1999).

Kits are semi-precocial, born fully furred with open eyes and erupted teeth (Baker and Hill 2003). Within minutes of birth, they are capable of swimming and exploring their surroundings, but they require a long period of parental care before they are self-sufficient. Kits begin to leave the lodge or den at about 2 weeks of age (Novak 1987) or as late as 6 to 8 weeks in Montana (Easter-Pilcher personal communication 2006). They are weaned at about 6 to 8 weeks (Bee et al. 1981, Jenkins and Busher 1979). Until they disperse at about age 2 years, kits depend on the family group for feeding, grooming, and maintaining dams and the winter food cache (Novak 1987).

Demography

For mammals in general and for rodents in particular, beavers are relatively long-lived, with small litter sizes and long periods of parental care. Females and males reach sexual maturity at age 2 years, and females generally bear their first litter at age 3 years (Larson 1967, Deems and Pursley 1983, Baker and Hill 2003). However, low population densities caused by heavy trapping pressure or environmental factors can hasten the age at which females first breed (Novak 1987). In heavily exploited, low-density populations in South Dakota and Ohio, approximately one third of females age 1.5 showed embryos or placental scars as evidence of breeding (Welch et al. 1993). Litter size usually ranges from two to five, occasionally up to nine, and averages three to four (reviewed by Baker and Hill 2003). Litter size varies with diet quality and the severity of winter weather (Jenkins and Busher 1979). In Colorado, average litter size was 2.7 above 5,000 feet elevation and 4.4 at lower elevations, probably due to increased quality of winter food (Fitzgerald et al. 1994). Litter size is also correlated with female weight (Wigley et al. 1983) and female age (Osborn 1953, Welch et al. 1993); it is generally smaller for females up to age 2 years, increasing to a peak at age 5 to 9 years, after which it decreases (Payne 1984c, Peterson and Payne 1986, Schulte and Müller-Schwarze 1999).

Fecundity is density dependent for all age classes, increasing as density decreases (Payne 1984c, Welch et al. 1993), and it is highest in the middle to older age classes. In exploited populations in Newfoundland, Payne (1984c) found the highest fecundity in beavers age 5 to 13 years. The lowest rate (0.32) was observed in yearlings, and the highest rate (1.80) was observed in the 10.5-year age class. The dominant female in a colony usually breeds every year regardless of habitat quality or population density (Novak 1987). Evidence of yearling females breeding has not been found in Region 2 states. Osborn (1953) reported pregnancy or evidence of reproduction in Wyoming beaver females of 0 percent for age 1.5 years, 21 percent for age 2.5 years, and 89 percent of age 3.5 years and older. In Kansas, Welch et al. (1993) found evidence of reproduction in 0 percent of yearling females and 50 percent for all females age 1.5 years and older; by age 4.5 years, all females showed evidence of reproduction.

Beavers in the wild live an average of 10 to 15 years (Wilson and Ruff 1999). However, most sex and age ratio data have come from trapping surveys or samples, which is biased by variability in trapping susceptibility and trappers' preferences among sex and age classes (Rutherford 1964, Henry and Bookout 1969). Sex ratios for most beaver populations approximate 1:1 (Baker and Hill 2003, Novak 1987), with reported ratios of 1.33:1 in South Dakota (Vanden Berge and Vohs 1977), 1.1:1 in Wyoming (Osborn 1953), and 1.13:1 in Idaho (Leege and Williams 1967). In some populations, sex ratios favor females with increased age, possibly due to increased mortality among males due to intraspecific competition (Provost 1958, Leege and Williams 1967).

Mortality rates for beaver populations in North America range from 22 to 39 percent (Payne 1984a). Bergerud and Miller (1977 in Olson and Hubert 1994) estimate that the mortality rate for age classes 2.5 years and older is about 30 percent. Mortality rates for beavers in Newfoundland were 52, 4, 40, 35, and 44 percent for age classes 0, 1, 2, 3, and 4, respectively, and 32 percent for all adults combined (Payne 1984b). The 52 percent mortality rate for the 0-year age class included intrauterine mortality. After birth, kits have a high survival rate due to protection by adults in the colony, but mortality increases during dispersal (Payne 1984b, Buech 1985 in Olson and Hubert 1994, Wilson and Ruff 1999). The most significant mortality factor for adults is human activity, especially trapping (Vanden Berge and Vohs 1977, Novak 1987, Wilson and Ruff 1999). Other human mortality factors include hunting, illegal shooting (Payne 1984b, Novak 1987), nuisance beaver control, habitat destruction (Henderson 1960), and killing by domestic dogs (Henderson 1960, Novak 1987). Principal environmental factors causing mortality include drought (Henderson 1960), severe winter weather and starvation in colder climates (Novak 1987), and extreme water fluctuations (Rutherford 1964, Novak 1987). Rare outbreaks of tularemia and other diseases sometimes decimate beaver populations locally (Novak 1987). Predation is not a significant mortality factor, except where beavers co-occur with gray wolves (*Canis lupus*). Intra-specific fighting and accidental death by tree-fall cause occasional mortality (Novak 1987).

Home range size of beavers depends on sex, age, colony structure, habitat, and seasonal constraints (Baker and Hill 2003). During summer, care of kits by females sometimes restricts female movements to a smaller area than adult males utilize. As kits become more independent in fall, adult home ranges may increase in size. In colder regions, ice may limit the size of winter home ranges. Habitat features strongly influence the size and shape of home ranges. A small pond may be occupied by a single colony with a roughly circular home range, while beavers living along streams and rivers typically have a more linear home range (Novak 1987). Territoriality exerts a strong influence on home range and population density, and it is probably responsible for a minimum intercolony distance of about 1 km observed in interior Alaska (Boyce 1981).

Beyond the distance limit imposed by territoriality, beaver population density is controlled by human exploitation (trapping), variations in natural mortality events such as predation or epizootic diseases, distribution of suitable habitat, and length of habitation time relative to available resources (a colony may deplete food resources over 10 to 20 years, then colonize a new area) (Hill 1982, Novak 1987). Reported colony densities range from near zero to at least 4.6 per km^2. Maximum colony density, or saturation point, in most habitats probably ranges from about 0.4 to 1.9 per km^2 (Baker and Hill 2003).

Genetic variability of beaver populations across the species' range is unknown, but it may be reduced from historic populations as a result of continent-wide beaver population depletions. Beavers are strong dispersers within and across watersheds, facilitating gene flow among populations. Extensive re-introduction and transplant operations have contributed to artificial gene flow.

Life cycle graph and population matrix analysis

We formulated a life cycle graph for the beaver that comprised nine stages (age classes). The model inputs (i.e., age-specific survival rates, fertilities, probability of breeding; **Table 1**) were selected from a review of the published literature (Payne 1984b, Payne 1984c, Novak 1987, Baker and Hill 2003). Adult survival rates were adjusted upward slightly from published rates to yield a population growth rate (λ) close to 1.0 (1.001), on the assumption that, in the long term, λ must be near 1 or the population will go extinct or grow unreasonably large (McDonald and Caswell 1993). From the resulting life cycle graph (**Figure 2**), we produced a series of matrix projection models with a post-breeding census for a birth-pulse population with a one-year census interval (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001). Here we present a summary of the model results; the complete technical analyses are shown in **Appendix**.

First, we conducted a sensitivity analysis. Sensitivity is the effect on λ of an absolute change in the vital rates (i.e., survival and fertility). The vital rates for which λ was most sensitive were first-year and second-year survival, followed by third-year survival. λ was less sensitive to changes in fertility rates than to changes in survival rates. Thus, we conclude from the sensitivity analysis that survival rates, especially for the first two age classes, are most important to population viability.

Next, we conducted an elasticity analysis. Elasticities help to resolve a problem of scale that can complicate conclusions drawn from the sensitivity analysis. Because survival rates and fertility rates are measured on different scales, interpreting the results of a sensitivity analysis can be somewhat misleading. Elasticities have the useful property of summing to 1.0.

Table 1. Parameter values for the component terms (P_i, B_i and m_i) that make up the vital rates in the projection matrix model for the North American beaver.

Parameter	Numeric value	Definition
m_2	1.55	Number of female offspring produced by a second-year female
m_3	1.8	Number of female offspring produced by a third-year female
m_4 to m_6	1.95	Number of female offspring produced by a "young adult" female
m_7 & m_8	2.1	Number of female offspring produced by an "older adult" female
m_9	1.9	Number of female offspring produced by oldest females
B_2	0.27	Probability of breeding in the second year
B_3	0.65	Probability of breeding in the third year
B_4	0.78	Probability of breeding in the fourth year
B_a	0.87	Probability of breeding as an "older adult"
P_{21}	0.58	First-year survival rate
P_{32}	0.42	Second-year survival rate
P_{43}	0.71	Third-year survival rate
P_a	0.87	Annual survival rate of "adult" females

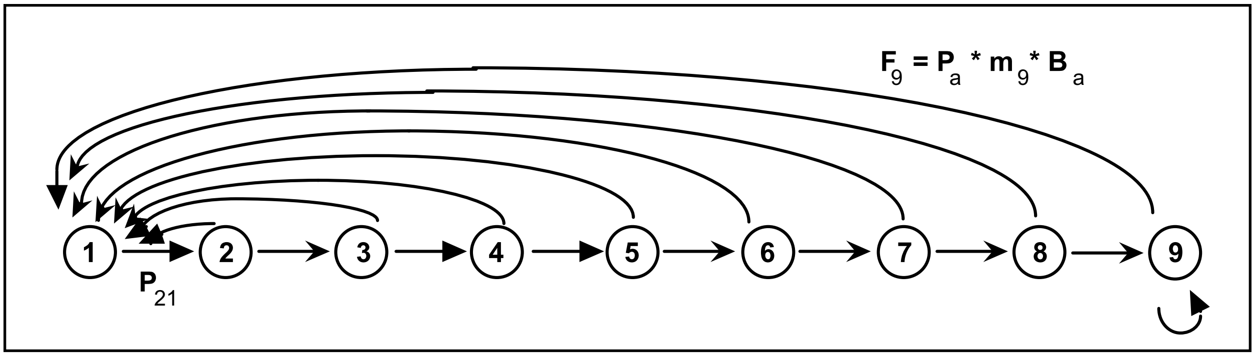

Figure 2. Life cycle graph for the North American beaver. The numbered circles ("nodes") represent the nine life stages (annual age classes). The arrows ("arcs") connecting the nodes represent the vital rates (transitions between stages). The horizontal arcs are survival transitions (e.g., first-year survival, P_{21}=0.58). The arcs pointing back to Node 1 represent fertility (e.g., $F_9 = P_a * m_9 * B_a$).

Elasticity analyses indicate that λ was most elastic to changes in first-year survival, followed successively by changes in survival of subsequent age classes. Overall, survival transitions accounted for approximately 81 percent of the total elasticity of λ. The sensitivities and elasticities for the beaver are consistent in emphasizing the survival transitions, and they indicate that survival rates of early age classes are the most important transition for population viability.

Finally, we constructed a stochastic model to predict the effect of stochastic (random) environmental variation on λ. Stochasticity was incorporated by varying different combinations of vital rates or by varying the amount of stochastic fluctuation. The stochastic model produced two major results. First, altering the survival rates produced a much greater change in λ than altering the fertility rates. Second, large-effect stochasticity has a negative effect on λ, at least when it affects transitions to which λ is highly sensitive. The negative effect on λ occurs despite the fact that average vital rates remain the same. These results indicate that beaver populations are relatively tolerant of stochastic fluctuations in production of offspring, but they are more vulnerable to fluctuations in the survival of early age classes (especially pre-breeding individuals).

Summary of major conclusions from beaver matrix projection models

- ❖ Survival accounts for 83 percent of the total "possible" sensitivity, with second-year survival the most important (24 percent of total) followed by first-year survival (20 percent). Any absolute changes in these survival rates will have major impacts on population dynamics.

- ❖ First-year and second-year survival account for 35 percent of the total elasticity, almost twice the total of the elasticities for all the fertility transitions. Proportional changes in early survival will have a major impact on population dynamics.

- ❖ The similarity between the conclusions from the sensitivity and elasticity analyses suggests that survival in the first 2 to 3 years of life is critical to population viability of beavers.

- ❖ Stochastic simulations echoed the other analyses in emphasizing the importance of early survival to beaver population dynamics, and showed that beaver populations are vulnerable to large variations in early age-class survival rates even if average rates remain constant over time.

Limiting factors

Limiting factors for beaver populations are typically habitat-related at local and landscape scales. Survival of young to dispersal age is closely related to colony size and the local environment, especially vegetation and stream variables. Availability of food resources is commonly limiting, as beavers often deplete resources over time within a usable foraging distance of impoundments. Post-dispersal survival and recruitment are related to dispersion of suitable habitat on the landscape, and at least to some degree on the suitability of connections between habitat patches (Easter-Pilcher personal communication 2006). Dispersal of subadult beavers limits local populations and is also the primary mechanism of population expansion, although secondary dispersal (emigration of adults) is also important (Sun et al. 2000, Baker and Hill 2003). At the metapopulation scale, the strong dispersal tendencies of beavers result in frequent colonization of new sites or abandoned colonies where food resources have recovered enough to support a new colony (Payne 1984a, Slough and Sadleir 1977).

Depending on habitat characteristics, a beaver colony may act as a source or sink population (Fryxell 2001). Source colonies are usually located in productive habitats with abundant high-quality food, resulting in high reproductive rates and large numbers of dispersing offspring that may establish new territories, become members of new breeding pairs, or reoccupy abandoned habitat. Sink colonies are usually located in poor quality habitats and have a low rate of reproduction and/or a high mortality rate. Sink colonies rely on immigration of dispersing beavers to stay active.

Community ecology

The principal ecological relationships between beavers and their environment are depicted an envirogram prepared for this assessment (**Figure 3**).

Predation

Beavers in established territories have few natural enemies due to the protection provided by the lodge or den and their aquatic habitat (Rutherford 1964). Only the gray wolf appears to exert significant predation pressure on beavers where the two species are sympatric (Wilson and Ruff 1999, Collen and Gibson 2000). Other common predators are mountain lions (*Felis concolor*), coyotes (*Canis latrans*), and domestic dogs (Henderson 1960, Novak 1987, Baker and Hill 2003). Other documented predators include lynx (*Lynx canadensis*), bobcat (*L. rufus*), black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), wolverine (*Gulo gulo*), mink (*Noevison vison*), river otter (*Lontra canadensis*), fisher (*Martes pennanti*) , large raptors, and even alligator (*Alligator mississippiensis*) in the southeastern United States (review by Collen and Gibson 2000). Beavers are more vulnerable to predation on land, particularly when they are dispersing, and transplanted beavers may be highly vulnerable to predation. McKinstry and Anderson (2002) reported that predators killed 71 percent of beavers transplanted in Wyoming; 38 percent were taken by coyotes, 14 percent by black bears, 14 percent by grizzly bears (*U. arctos*), 3 percent by mountain lions, and 31 percent by unknown predators.

Competition

Large herbivores such as deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) may compete with beavers for riparian vegetation. These species may reduce beaver food supply by eating shoots of aspen and other woody species, or by trampling willow stands and suppressing stand reproduction (Rutherford 1964). Livestock, especially cattle, grazing in riparian areas can also degrade beaver habitat by removing woody vegetation (Apple 1985). Where top-order carnivores such as wolves occur, they can indirectly benefit beaver populations by influencing the distribution and behavior of elk, which in turn can release woody vegetation in riparian areas from ungulate overbrowsing (Beschta 2003). In Rocky Mountain National Park, where high elk numbers have coincided with beaver population declines, Baker et al. (2005) used field experiments to study the interaction of elk and beaver herbivory on willow stands. They found that elk browsing combined with beaver cutting strongly suppressed the standing crop of willow, which was better able to withstand either elk browsing or beaver cutting alone. They predicted that intense herbivory by wild ungulates or livestock on willow or similar riparian woody species can disrupt naturally occurring beaver-plant mutualisms, reduce the availability of winter beaver food, and thus reduce beaver populations.

Parasites and disease

Parasitism in beavers is of minor significance. Endoparasites include stomach nematodes and intestinal flukes. Ectoparasites include ticks, leeches, and beaver beetles (Rutherford 1964, Novak 1987). Beavers may serve as hosts for the intestinal parasite *Giardia lamblia* (Olson and Hubert 1994), which can affect humans and domestic animals.

The only disease known to affect beaver populations significantly is tularemia, a water-borne bacterial disease caused by *Francisella tularensis* biovar. *palaearctica* (type B) that affects the liver, spleen, lungs, and lymph nodes. Usually an infection causes no noticeable effect on an individual beaver, but occasional epizootic outbreaks can cause mass mortality (Baker and Hill 2003). Tularemia affects beavers, muskrats (*Ondatra zibethicus*), and other semi-aquatic mammals (Novak 1987). Beavers may carry fecal coliform bacteria, and increased water temperature in impoundments may improve growing conditions for intestinal and non-intestinal coliform (Bates 1963).

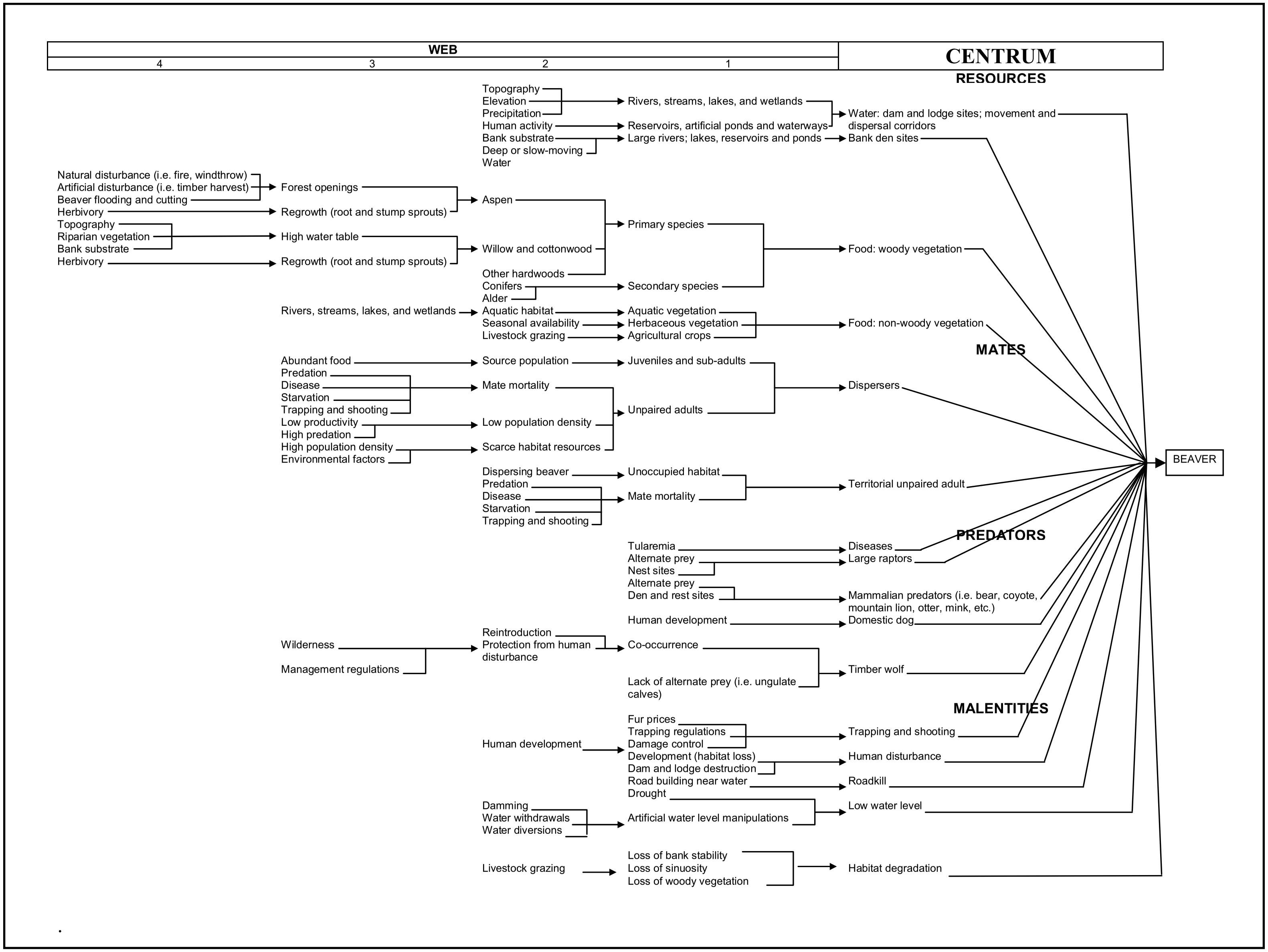

Figure 3. Envirogram of the North American beaver.

Symbiotic and mutualistic interactions

Beavers are a habitat-modifying keystone species whose effect on the landscape influences the survival of many plant and animal species (Rosell et al. 2005). Their effects on habitat are unmatched by any other species in their range, and their presence is pivotal for maintaining community organization and species diversity in many riparian systems (Mills et al. 1993, Baker and Hill 2003). The beaver's impact on ecosystem processes includes alterations in hydrology, biogeochemistry, vegetation, and ecosystem productivity (Naiman et al. 1988). In the short term, beaver cutting of woody vegetation can reduce or eliminate tree cover especially near the lodge or pond; tree species may be depleted to the point that beavers abandon the site, while at least some willow stands may be inhabited indefinitely (Baker and Hill 2003). In the long term, beaver damming activity promotes sediment accumulation, promotes water conservation by reducing runoff efficiency, and provides ideal colonization sites for herbaceous and woody riparian vegetation. Beaver herbivory on willow results in a mutualistic interaction in which beaver cutting stimulates willow growth patterns beneficial to beavers and other browsers, at least in the absence of intense browsing by ungulates (Baker et al. 2005). Beaver presence enhances invertebrate production (McDowell and Naiman 1986) and increases the complexities of ecosystem boundaries (Johnston and Naiman 1987), increasing microhabitats (Wilsson 1974) and typically increasing species diversity (Emlen 1973).

Habitat modifications by beavers benefit a large number of wildlife species that depend on aquatic, wetland, or riparian habitat for all or part of their lifecycle (review in Baker and Hill 2003). Wet meadows and willow carrs of the middle and higher elevations in Region 2 are often the result of beaver activity; these features form over time as beaver ponds fill with silt. The benefits of beaver activity to other wildlife increase over time as wetland and water surface areas increase (Schulte and Müller-Schwarze 1999).

Birds: Beaver-created ponds and wetlands provide important feeding, breeding, wintering, and migration habitat for waterfowl and other waterbird species. Ponds and associated wetland vegetation provide courtship areas, nesting cover, aquatic plants and invertebrates as food resources, and travel lanes for birds and their broods through beaver transport channels (Ringelman 1991, McKinstry et al. 2001). Larger beaver complexes can provide significant stopover habitats for migrating waterfowl and shorebirds. Beaver cutting opens the forest canopy and improves habitat for edge and woodland species such as blue grouse (*Dendragapus obscurus*), wild turkey (*Meleagris gallopavo*), and songbirds (Novak 1987). Flooding and girdling create snags that provide insect food and nest cavities for woodpeckers and secondary cavity nesters (Wessels 2001). Reintroduction of beavers to a Wyoming site increased avian species richness by 20 percent (Apple 1985), and Hair et al. (1979) found higher numbers of bird species in beaver impoundments than in adjacent pine and hardwood forests.

Mammals: Beaver-modified riparian areas create or enhance habitat for other semi-aquatic mammals. Muskrats and mink inhabit beaver impoundments and benefit from increased prey and forage resources. Muskrats sometimes shelter in beaver lodges, even while occupied by beavers (McKinstry et al. 1997). River otters make extensive use of beaver-created habitat features (Polechla 1989), and interactions between beavers and river otters may strongly influence both species where they co-occur. Otters in beaver-modified habitats benefit from a more stable water supply, increased vegetation cover, and enhanced abundance of fish prey. Otters often shelter in beaver lodges and bank dens, including use as natal dens (Polechla 1989). River otters may influence beavers by occasionally breaching beaver dams, driving beavers from dens and, rarely, preying on beaver kits (Reid et al. 1994).

Beaver-modified riparian areas also influence habitat for terrestrial mammals. Creation of early seral stage forest openings and development of riparian shrublands typically increase forage and cover for deer and elk (Grasse and Putnam 1955, Apple 1985). Moose benefit from increased production of woody plants and aquatic vegetation (Baker and Hill 2003). In Idaho, small mammal biomass was two to three times higher in beaver-influenced willow shrublands than in adjacent riparian habitat (Medin and Clary 1991 in Baker and Hill 2003). Small mammal abundance, in turn, increases prey resources for many species of carnivorous reptiles, birds, and mammals.

Fish and other aquatic life: Effects of beaver activity on fish populations depend on initial stream conditions (Wilson and Ruff 1999, Collen and Gibson 2000). Beaver impoundments can often benefit fish by increasing aquatic habitat area (Olson and Hubert 1994), improving water quality, reducing erosion (Collen and Gibson 2000), and reducing fluctuations in seasonal flows (Call 1966). Increased water depth may improve overwinter fish survival (Call 1966, Olson and Hubert 1994) by providing cover and resting habitat and reducing temperature fluctuations. Beaver food caches and debris from lodges and dams provide fish cover and foraging areas for predatory fish (Collen and Gibson 2000).

In warm streams at low elevations, increased temperatures from beaver activity may harm some fish populations, particularly sport salmonids (Hill 1982, Munther 1983) by decreasing dissolved oxygen or lowering pH (Novak 1987). In small, cold streams of mountainous regions, increased temperatures may provide better conditions for optimal fish growth and development (Munther 1983, Collen and Gibson 2000).

Beaver activity can cause varying effects on fish spawning habitat and fish movement. In some situations, reduced stream velocity can increase deposition of coarse sediments important for salmonid spawning beds (Kondolf et al. 1991 in Collen and Gibson 2000), but spawning habitat can also be degraded or destroyed by siltation or excessively deep water in ponds (Call 1966, Swanston 1991 in Collen and Gibson 2000). Beaver dams may form partial or total barriers to fish seasonal movements or dispersal (Call 1966, Novak 1987, Collen and Gibson 2000), an effect that may be considered harmful or beneficial, depending on the fish species and desired conditions (e.g., managed sport fish vs. undesirable introduced species).

Landscape ecology

Because of their extensive habitat modifications, beavers exert a strong influence on their environment (review by Rosell et al. 2005). Beavers affect the structure and function of adjacent terrestrial ecosystems by reducing vegetation height and selectively cutting preferred species (Naiman et al. 1988), which alters the growth form and stand density of cut vegetation (Barnes and Dibble 1986, Dieter 1987). Cutting opens gaps in the forest canopy that favor shade-intolerant species preferred by beavers, particularly aspen (Novak 1987, Fryxell 2001). If beaver herbivory is sufficiently intense, however, understory saplings and root or stump sprouts of preferred species are consumed, reducing the abundance of beaver food as less preferred and shade-tolerant species such as conifers become established (Rutherford 1964, Fryxell 2001).

On a landscape scale, beaver activity can influence fish community species composition and interspecific interactions by altering channel morphology (including riffle-pool ratios) and changing invertebrate species composition and abundance (Collen and Gibson 2000). Beaver impoundments may also increase the abundance of fish predators such as river otter, mink, herons, mergansers, kingfishers, and predatory fish species (Novak 1987, Collen and Gibson 2000).

Beaver damming in streams influences flooding dynamics, sediment transport, and water storage and release patterns (review in Baker and Hill 2003). By moderating flooding, increasing water storage, and evening water release during drier periods, beaver activity provides ecological benefits. Damming facilitates the establishment of riparian vegetation by increasing the extent and duration of soil moisture, and by providing sediment for seedling establishment (Baker and Cade 1995). Willows, sedges, and other plants associated with a high water table replace conifers, hardwood trees and shrubs, and other vegetation that cannot survive flooding (Rutherford 1964). Impoundments generally increase habitat for shallow rooted aquatic and floating plants. Beaver-modified riparian areas create habitat for numerous wetland plants, including many species of conservation concern in Region 2 because of rarity or endemism. Economic benefits also result from the ecological impacts of beaver activity. Decreased catastrophic flooding, increased water storage, and more even release of water from headwater areas during summer are all likely to benefit downstream agricultural users. Enhanced wetlands, wildlife habitat, and fish habitat have positive effects on sport hunting and fishing activity.

CONSERVATION

Threats

Historically, the greatest threats to beavers in Region 2 were overharvesting by the unregulated fur trade from the early 1800's to the early 1900's, coupled with extensive degradation of riparian areas by livestock overgrazing and other human land uses during the late 1800's to early 1900's. The most serious remaining threat to beavers region-wide is loss and degradation of habitat to human land uses including water manipulations, livestock grazing in riparian areas, and urban and agricultural development in riparian areas. Beaver damage control to mitigate human-beaver conflicts is a threat locally in agricultural and urban areas. Illegal trapping and shooting occurs but is not regarded as a threat to populations.

Stream volume and flow perturbations

Water development for agricultural and urban uses profoundly affects water volumes and seasonal flow patterns of most rivers and streams in Region

2. Dewatered stream reaches cannot support beavers. Reduced flows can expose lodge or den entrances and food caches, decreasing accessibility of beavers to shelter and leaving them more vulnerable to predation. Increased flows may flood lodges and dens, or wash away food caches, dams, and lodges. Rapid fluctuations in flows associated with a hydroelectric dam had a catastrophic influence on a population of *Castor fiber* in Sweden (Curry-Lindahl 1967 in Gurnell 1998). Low flows in early fall can stimulate dam building on unbraided or straight river sections where beavers normally would not build dams (Martin 1977).

Streamflow alteration can also indirectly affect beaver habitat. Reservoirs typically reduce peak flows and trap sediments, altering sediment deposition patterns downstream (Martin 1977). These factors contribute to changes in channel morphology and riparian vegetation that may affect the quality and quantity of beaver habitat. Martin (1977) reported that the free-flowing Yellowstone River supported a higher density of beavers (0.87 colonies per km) than did the impounded Tongue or Bighorn rivers (0.63 and 0.55 colonies per km, respectively). The impounded rivers had lowest beaver densities immediately below the dams, where stream sections had a single channel with few deciduous trees or shrubs. Incised streams are common in Region 2 and are often the result of human activity. Stream down-cutting can be caused by removal of riparian vegetation leading to loss of channel stability, channelization for water diversion or flood control, channel constriction by undersized culverts or placement of roads or facilities, release of sediment-free water from impoundments, or artificial increases in flow that exceed the capability of the channel to handle the new flow regime or stream power (Vacirca personal communication 2005). Stream incision can lower the floodplain water table, reduce floodplain area, and cause the loss of riparian vegetation critical for beaver food and construction materials.

Streamflow perturbations pose the greatest threat to beavers on lower flow streams that supply water to agricultural lands or urban areas. In many of these watersheds, diversions cause near or complete dewatering of streams during the growing season. In such depleted systems, beaver habitat may be limited to artificial water bodies such as irrigation ditches, ponds, and areas where agricultural return flows create wetlands on the river floodplain.

Habitat destruction

Destruction of riparian habitat is most pronounced in low-elevation areas subject to intensive agriculture and urban development (Buskirk 2000). Residential and commercial development is often concentrated along rivers and lakeshores in Region 2 due to topography, land ownership patterns, and scenic and fishing amenities. Development that reduces woody deciduous vegetation or riparian cover and structure adversely affects beaver habitat suitability by reducing the quality and availability of food and construction materials.

Stream channelization reduces the area of suitable beaver habitat in braided stream systems, and increases in stream velocity can destroy dams and lodges downstream, which may render stream reaches uninhabitable (Martin 1977). Armoring stream banks with riprap or other construction materials can prevent beavers from building bank dens and lodges. Dredge mining operations in streams temporarily destroy existing beaver habitat, and can trigger changes in stream morphology that degrade or even destroy beaver habitat for many years or considerable distances downstream.

Grazing by livestock and wild ungulates

Improperly managed livestock grazing in riparian areas can reduce riparian shrub and tree vegetation by browsing and trampling. Livestock use in riparian areas also can cause bank erosion and stream down-cutting (Elliott et al. 1999), which leads to a lowering of the water table, reduction in floodplain area, and degradation or elimination of woody riparian vegetation. Excessive browsing of woody riparian vegetation by wild ungulates, particularly elk and moose, can also reduce the quality and abundance of beaver food (Kay 1994). Trampling and browsing by large herbivores can suppress aspen reproduction along streams and reduce beaver food availability (Rutherford 1964).

Beaver damage control measures

Beaver populations generate a significant number of damage complaints in all states except Wyoming. Where beavers occur in developed or agricultural areas, beaver activity often comes into conflict with human land uses. Beavers can damage or destroy ornamental trees, agricultural crops, and timber resources.

Damming may flood roads, forests, agricultural land, and residential or commercial property, and interfere with water flow in road culverts, ditches, and irrigation control structures (Deems and Pursley 1983, Novak 1987, Olson and Hubert 1994, Wilson and Ruff 1999). Occasionally, beavers may build dams on unstable shale formations or steep headwater streams, thus increasing the potential for severe erosion and stream channel downcutting from catastrophic dam failure (Retzer et al. 1956, Gurnell 1998). Beaver ponds can increase breeding areas for mosquitoes or harbor disease organisms such as *Giardia lamblia* (Olson and Hubert 1994, Schulte and Müller-Schwarze 1999).

Various methods are employed to control nuisance beavers. Lethal control methods include trapping and shooting, permitted in all Region 2 states within state-established regulations. Breaching dams is commonly employed to discourage beaver damage, but beavers tenaciously rebuild. Destroying dams and lodges may harm beavers by increasing predation, reducing accessibility of food resources, or decreasing winter survival. Nuisance beavers are sometimes captured and transplanted to other areas, but poor survival of transplanted beavers is likely unless transplants are implemented carefully. Damage control measures can substantially reduce beaver populations in certain areas through direct mortality, reduced survival for wintering beavers or dispersers forced to locate new territories, and decreased reproduction through breaking up pairs or disrupting breeding and kit rearing.

Illegal trapping and shooting

Illegal shooting and trapping of beavers may impact beaver populations locally. Trappers in Newfoundland reported evidence of shooting in up to 18 percent of captured beavers, representing only beavers that survived shooting injuries. Trappers have reported observations of duck and ptarmigan hunters using beavers for target practice (Payne 1984b).

Other threats

Other detrimental factors may affect beavers locally but are not substantial threats region-wide. Water quality is not a significant limiting factor for beaver habitat, but beavers may be killed by severe pollution such as oil contamination, or discouraged from occupying water polluted by salt, sewage, or harmful chemicals (Henderson 1960). Recreational facilities and trails that encourage human use along waterways also introduce dogs, which may disrupt beaver activity or rarely kill beavers. Roadkill is an occasional source of mortality where roads cross or approach beaver habitat.

Landscape-scale threats

A potential landscape-scale threat to beavers is habitat fragmentation caused by human development and associated water development projects. Beaver distribution over time is necessarily dynamic as family groups often deplete food resources and move to new colony sites. Beaver habitat in Region 2 is mostly confined to stream and river systems that are infrequent on the landscape because of low precipitation or natural fragmentation by mountainous terrain. Additional fragmentation of beaver habitat by human development and land uses may affect beaver dispersal, reducing the ability of family groups to locate new sites or for populations to interact and expand into suitable habitat. Reduced dispersal capability may also reduce gene flow across the landscape. However, beavers are highly capable dispersers even across large areas of unsuitable habitat and can adapt to human-altered habitats as long as basic resource needs are met. Beavers are readily transplanted, which facilitates artificial gene flow. Consequently, landscape-scale threats are not likely to be substantial for beavers.

Conservation Status of the North American Beaver in Region 2

Distribution and abundance of beavers in Region 2 are generally reduced from historic levels by past overharvest and ongoing habitat degradation. Nonetheless, beavers are once again relatively common in many areas where suitable aquatic and riparian habitat remains. Populations appear stable or increasing as remnant and reintroduced populations expand to occupy remaining habitats in their historic range (Novak 1987, Baker 2003). While quantitative data are on beaver distribution and population trend are mostly nonexistent in all Region 2 states, beavers are easily observed and anecdotal information is considered adequate for all Region 2 state wildlife agencies to conclude that beaver populations are viable statewide, and expanding in some areas.

While overall population viability is not a concern in the region, areas of potential habitat remain unsuitable for beavers because of past or current human land uses. On some public lands, including some National Forest System lands, beavers remain absent or reduced in abundance because of incised stream channels, degraded riparian vegetation, or altered streamflow regimes. On private lands these habitat problems also persist, along with increasing human development in riparian areas. Restoring beaver populations to their maximum viability on public lands is desirable because of the beaver's capability to restore and maintain riparian ecosystems. Protection of beaver populations (including restoration where necessary) on National Forest System units where the beaver is a designated MIS is particularly important in order to meet the second objective of MIS designation (to monitor the effect of management actions on riparian/aquatic species). Currently, riparian condition inventories are not available at broad scales to assess the viability of beaver habitat across the region, but all Region 2 National Forest System units are likely to have areas where incised stream channels, altered streamflow regimes, and degraded riparian vegetation limit beaver occupancy. Preventing further habitat degradation and restoring degraded habitats will be key to protecting and restoring beaver populations on National Forest System lands.

Demographic patterns of the beaver contribute to both vulnerability and robustness of species persistence. Beavers have a relatively low biotic potential due to small litter size and the long juvenile development period. Furthermore, the population matrix analysis (**Appendix**) indicates that survival of 1st and 2nd year juveniles is the most critical factor in population viability. Survival of these age classes partly depends on the ability to successfully disperse and recolonize vacant habitats that have recovered from past abuse. On the other hand, beavers are strong dispersers, and reproduction increases in response to low population density; these factors help beaver populations to recover quickly from local reductions and to colonize new areas. Human land uses that fragment beaver habitat by imposing barriers to beaver movement may increase mortality of dispersing beavers and reduce the distribution and abundance of beavers on the landscape.

Management of the North American Beaver in Region 2

Implications and potential conservation elements

Because beavers are widespread and populations appear to be stable or increasing where suitable habitat exists in many areas of Region 2, the primary conservation concerns are to ensure that existing beaver populations remain viable and to restore beaver populations to unoccupied habitat where appropriate to take advantage of their capability to restore and strengthen the ecological integrity of aquatic and riparian ecosystems. Because the beaver is a MIS for some National Forest System units in Region 2, their existence in those units is of special importance to forest monitoring and planning.

Maintaining viable populations

The most important threats to the viability of beaver populations in Region 2, particularly on public lands, are habitat-related. Human population growth in most of Region 2 is escalating demands on water resources, and the increasing need for water storage and diversion projects further degrades beaver habitat. Human population growth in the region is also leading to increased human development in riparian areas, further degrading beaver habitat and increasing human-beaver conflicts and the need for damage control efforts that reduce or eliminate beaver populations. Excessive grazing by livestock (and in some areas by wild ungulates) continues to degrade riparian habitat for beavers on public and private lands. Maintaining the current beaver populations across broad areas of Region 2 will require management and mitigation of these habitat threats.

Beaver management plans must take into account landscape-scale habitat management. To maintain viable populations, managers should ensure that land uses maintain connectivity between watersheds to facilitate long-range dispersal and gene flow. This scale of management maintains metapopulation dynamics and allows natural dispersal to repopulate watersheds where beavers have been reduced or extirpated by natural or human causes. On a smaller scale, management activities should ensure that beaver colonies can move freely within watersheds so that they can colonize new areas as resources are depleted at existing colony sites. This allows vegetation to recover from beaver herbivory, and reduces the potential for habitat degradation from overutilization by beavers unable to make secondary dispersal movements. Examples of landscape-scale land uses that account for beaver habitat management include forestry practices that promote the growth of early successional species preferred by beavers such as aspen, and water development projects that ensure adequate flows during beaver dispersal periods and seasonal flow regimes that protect riparian vegetation.

At project-level scales, management practices that potentially affect riparian vegetation and stream hydrology or morphology should mitigate adverse impacts to beaver habitat, and enhance beaver habitat where possible. Region 2 handbooks and other USFS directives require all Region 2 units to comply with practices to protect aquatic and riparian habitats during implementation of USFS projects and plans. Thus, forest planning goals for all Region 2 units specify monitoring and protecting aquatic, wetland, and riparian habitats, which benefits beaver habitat. The Bighorn National Forest Draft Forest Plan Revision (2004) documents the importance of beavers in riparian system functioning, and their role as a keystone species providing habitat for other species. The plan addresses the management challenges of reduced beaver distribution and abundance, species reintroduction efforts, and possible disease interactions affecting beavers in the Bighorn National Forest. The Plan also outlines a beaver population monitoring protocol (food cache inventory from aerial or ground surveys) and the need to maintain adequate beaver habitat in the presence of forest management actions, including grazing, road maintenance, and recreational use. The Black Hills National Forest Plan (1997) lists Riparian Areas Seral Stage and Trend as a habitat component that will be monitored. The Grand Mesa, Uncompahgre, and Gunnison National Forest 2002 Annual Monitoring and Evaluation Report states that riparian areas are being managed on this forest to achieve the latest possible seral stage within stated project objectives.

On state and federally managed lands, control of ungulate game populations through hunting and habitat management and sound rangeland management practices for domestic livestock can reduce competition and habitat degradation by large herbivores. Forestry practices that avoid removing woody vegetation near suitable beaver streams can protect beaver food resources. In watersheds influenced by water development projects, water withdrawals and flow manipulations can be planned to minimize impacts on beaver habitat.

Maintaining viable beaver populations also requires ensuring the sustainability of commercial harvest. Beavers are vulnerable to overharvest because of the relative ease of capture, their dependence on aquatic habitat, delayed sexual maturity, and a slow reproductive rate (Baker and Hill 2003). Commercial harvest of beavers in Region 2 is managed by state wildlife agencies, except in Colorado where commercial harvest is effectively precluded by the state constitution. Strict regulations and harvest monitoring by other Region 2 states are adequate to ensure that commercial trapping is not excessive, and erratic and low pelt prices since the 1980's have reduced commercial harvest levels (Novak 1987, Baker and Hill 2003). State management plans need to continue to account for overharvest vulnerability to ensure that local or regional populations are not decimated by excessive exploitation.

Beavers as a restoration tool

The capability of beavers to store water, trap sediment, reduce erosion, and enhance riparian vegetation can be used as a management tool to restore degraded aquatic and riparian ecosystems (Baker and Hill 2003, Müller-Schwarze and Sun 2003, Rosell et al. 2005). Beavers are a habitat-modifying keystone species and play a pivotal role in influencing community structure in many riparian and wetland systems (Mills et al. 1993). However, beavers occupy a broad range of habitat types and situations across Region 2, and they may not have a significant influence on ecosystem structure and function in every instance. The strength of beavers' impact on aquatic and riparian systems depends on the geographical location, topographic relief, and various vegetation and aquatic characteristics (Rosell et al. 2005). Managers should carefully evaluate a site's potential to be influenced by beavers before initiating beaver management for ecosystem restoration.

Beavers alter ecosystem hydrology, biogeochemistry, vegetation, and productivity (Naiman et al. 1988), with consequent effects on the plant, vertebrate, and invertebrate populations that occupy beaver-modified landscapes. In the arid West, riparian habitats typically cover less than 1 percent of the total land surface (Apple 1985). The sagebrush steppes of Wyoming in Region 2 underscore the importance of the beaver's keystone role; an estimated 75 percent of all wildlife supported by this ecosystem depend on beaver-enhanced riparian habitat (Smith 1982 in Olson and Hubert 1994).

Beaver impoundments trap fine textured sediments that act as water storage reservoirs (Retzer et al. 1956), resulting in slow, sustained discharge that maintains streamflows during dry periods (Parker et al. 1985, Olson and Hubert 1994); afford protection from flooding of downstream areas (Olson and Hubert 1994); and produce a raised water table that enhances riparian zones and extends the growing season (Apple 1985). In arid ecosystems where streams may become dry in the summer months, water impounded behind beaver dams may provide the only above ground water source for wildlife and livestock (Rutherford 1964). In Wyoming, beaver-impounded streams were associated with an average 3.4 ha of wetlands, compared with an average 1.1 ha of wetlands in streams without beavers (McKinstry et al. 2001). In the mountains of Montana, Munther (1982 and 1983 in McKinstry et al. 2001) observed up to 9.6 ha per km of wetlands in beaver-occupied streams, compared with an average of 0.8 to 1.6 ha per km for all streams in the region. Beaver dams and flooding provide a barrier protecting riparian vegetation from cattle and native ungulates (Olson and Hubert 1994), and beaver herbivory has been shown to increase growth and density of riparian vegetation, especially willow, by stimulating root and stem sprouting (McGinley and Whitham 1985, Dieter 1987, Barnes and Dibble 1988).

Beaver habitat modifications can reduce pollution and improve water quality in aquatic ecosystems. In the arid West, non-point source pollution is a major threat to water quality (Maret et al. 1987). An estimated 80 percent of all nutrients entering the Flaming Gorge Reservoir in Wyoming are from non-point sources (Southwestern Wyoming Water Quality Planning Association 1978 in Maret et al. 1987). Beaver impoundments can improve water quality by reducing pollution from sewage, livestock, and agricultural discharge (Balodis 1994 in Collen and Gibson 2000); trapping sediment and nutrients (Parker et al. 1985, Maret et al. 1987); reducing downstream turbidity (Bates 1963); and purifying water from acid mine drainage (Hill 1982).

Mechanical restoration of incised stream channels can be expensive and labor-intensive, making natural restoration by beavers an attractive alternative (Baker and Hill 2003). When beavers are re-established into degraded riparian ecosystems, eroded gullies are transformed into a network of ponds and wetlands that slow erosion, trap sediment, and raise the water table, allowing both the channel and riparian vegetation to recover (Apple 1985, Olson and Hubert 1994, Wilson and Ruff 1999). Beavers have been used extensively in Wyoming (Apple 1985, Olson and Hubert 1994, McKinstry and Anderson 1999, McKinstry et al. 2001) and Oregon (Stack and Beschta 1989 in Collen and Gibson 2000) to restore degraded streams impacted by livestock grazing. Beaver impoundments provide conditions that facilitate the establishment of vegetation in strip-mined areas (Hill 1982). Beavers may also help to control invasive non-native vegetation such as tamarisk. In northwestern Colorado, beavers selectively cut tamarisk to build their dams, and beaver impoundments created conditions that favored increased distribution and abundance of willow over tamarisk (B. W. Baker unpublished data in Baker and Hill 2003).

Economic benefits

Beaver-created wetlands and ponds provide improved hunting and fishing opportunities, and increased recreational opportunities such as boating, swimming, and wildlife viewing (Hill 1982, Munther 1983, Novak 1987). Commercially, beavers are harvested for their fur pelts and to provide castoreum for the perfume industry (Rutherford 1964, Deems and Pursley 1983). The beaver's ecological role on the landscape can help to protect property from flood damage and to improve agricultural production through increased groundwater storage (Baker and Hill 2003). "The ecological role of beaver…has tremendous indirect economic benefit [that] may far outweigh the monetary value obtained from their fur, and may offset any direct or indirect costs due to beaver damage" (Baker and Hill 2003).

Tools and practices

Inventory and monitoring

Inventory may include any qualitative or quantitative assessment of beaver populations or habitat. Monitoring generally means the repeated assessment of a population or habitat for the purpose of detecting change within a defined area over time (Thompson et al. 1998). When designing a program for inventory or monitoring, goals and techniques need to be carefully defined. Effective monitoring must entail robust sampling over spatial and temporal scales, using methods that permit detectability estimates and identify sources of variance.

Various population inventory and monitoring techniques provide information on beaver presence, relative abundance, or absolute abundance. Relative abundance is measured by an index, such as number of active food caches observed, to indicate population trend. Beavers are relatively difficult to observe directly because of their aquatic and nocturnal habits, but beaver sign is easily seen and provides the basis for several relative abundance techniques.

Beaver population density can be expressed as the number of colonies or individuals per unit area (in broad wetland habitats) or unit length of stream or shoreline (more appropriate in most of Region 2). The number of individuals is often estimated from colony counts, but the estimate is only meaningful if the mean number of individuals per colony is determined from local data, often a difficult task (Novak 1987, Baker and Hill 2003). Colony size can be sampled in the field by counting beavers with night-vision scopes (Easter-Pilcher 1987), driving beavers from their lodges or dens with smoke or dogs, or attempting to trap all the beavers in a colony; the last is difficult to accomplish and provides a conservative estimate (Baker and Hill 2003). Where sufficient harvest data exist, mean colony size can also be estimated from models using age and reproductive data (Novak 1987) or the relationships among natality, mortality, and dispersal (Bishir et al. 1983). Size of the winter food cache has been evaluated for use as an index of colony size, but this requires further study (Baker and Hill 2003). Easter-Pilcher (1990) found that food cache size was a significant predictor of colony size in northwestern Montana, but Osmundson and Buskirk (1993) found it was a poor predictor in Wyoming. Swenson et al. (1983) reported that aerial surveys along prairie rivers in Montana found 90 percent of beaver food caches, but they concluded that cache surveys alone were not adequate to estimate population size or trend because of variability in colony sizes.

Aerial surveys are most often used to estimate beaver distribution and abundance, because large or remote areas can be quickly surveyed. However, the efficiency, accuracy, and precision of aerial surveys can be highly variable (Novak 1987). Results depend on search methods, terrain, vegetation, and behavior of beavers (Hill 1982, Novak 1987). Aerial surveys are better suited to streams and wetlands where beavers build dams, lodges, and food caches that can be readily seen. Aerial surveys of Kansas rivers where beavers occupied bank dens and did not build food caches found only 41 of 146 ground-located beaver colonies (Robel and Fox 1993). Difficulties in distinguishing between active and inactive beaver sign form the air also can introduce considerable bias into aerial surveys.

Aerial photographs are useful for identifying beaver habitat for later ground or aerial survey, and at fine scales, they can be interpreted to locate beaver sign such as ponds and dams. Global position system (GPS) devices can be incorporated into ground or aerial surveys to plot exact locations of beaver colonies or sign, and data can be integrated into geographic information systems (GIS) to spatially model beaver habitat and distribution (review in Baker and Hill 2003). Aerial videography is a rapidly advancing technology that can be used to map and monitor beaver activity (Baker and Hill 2003). Videography can be used with GPS to link imagery with time and location data for GIS analysis. Helicopter videography is more useful in some situations such as sharply meandering stream systems or canyons that are difficult for fixed-wing aircraft to navigate.

In Region 2, states monitor population trends mainly through harvest data reports, except in Colorado where beavers are not commercially harvested. The Wyoming Game and Fish Department stopped conducting harvest surveys in 2003 due to low trapper response (Rothwell personal communication 2004). In Kansas, harvest data are used to evaluate trends, but the Kansas Department of Wildlife and Parks plans to implement a regular population monitoring program for beavers using canoe surveys in the future (Peek personal communication 2004). Use of harvest data to infer population trends is tenuous because of inherent bias caused by variations in trapping effort due to fluctuating fur prices and other factors (Novak 1987). South Dakota is the only Region 2 state that estimates the relative abundance of beavers based on annual wildlife survey data rather than harvest reports (Kiesow personal communication 2004).

Inventory and monitoring of beaver habitat can be accomplished by a combination of assessments of existing data and field observations. Existing vegetation and hydrological mapping of National Forest System lands can be used to delineate potential beaver habitat in streams, wetlands, and lakeshores. Interpretation of standard and infrared aerial photos is useful for identifying riparian habitat features, including vegetation cover and density, stream and floodplain width, channel and bank stability, and size of total riparian area (Cuplin 1985). Ground-truthing is important for accurate aerial photo interpretation (Dickinson 1971, Cuplin 1985). Monitoring beaver habitat requires defining and measuring habitat variables important for beaver occupancy; these factors vary locally and should be chosen to represent the habitat factors important in the area of concern, as well as the efficiency and cost of monitoring the habitat characteristics. An HSI model (Allen 1983) provides a useful list of potential habitat characteristics for monitoring; these include riparian vegetation characteristics (canopy cover, height, stem diameter, and species of trees and shrubs), stream gradient, water level fluctuation, and (for lakes) ratio of shoreline length and lake area. The HSI model provides a numeric index of habitat suitability that can be calculated periodically from monitoring data to determine trends in habitat suitability. Baker and Cade (1995) developed a logistical model to predict willow biomass based on stem diameter class to estimate beaver food in order to evaluate beaver carrying capacity in mountainous Colorado habitat. To more accurately model beaver food availability in willow-dominated areas, the HSI model could be modified to incorporate the willow biomass model.

USFS Region 2 has developed ecosystem function assessment methods for riparian and aquatic ecosystems. When available, data from these assessments will provide information on aquatic and riparian function specific to National Forest System lands. The data may provide the most comprehensive information for assessing beaver habitat capability across entire National Forest System units. Assessment of proper functioning condition for riparian areas (Prichard 1998) has been widely applied for assessing ecological health of riparian areas on National Forest System and BLM-administered lands in Region 2. Data from these assessments can be adapted to monitor trends in beaver habitat suitability.

Habitat protection can include a vast number of measures and practices. The USFS Watershed Conservation practices Handbook (Forest Service Manual 2509.25, available online at http://www.fs.fed.us/cgi-bin/Directives/get_dirs/fsh?2509.25), provides a comprehensive set of management measures addressing hydrologic function, riparian areas, and soil and water quality.

Capture and marking

Beavers can be captured alive using Hancock or Bailey traps, box traps, or various types of snares or nets (Baker and Hill 2003). Hancock traps are the most widely used devices, but they can be dangerous for humans to set because of their large size and powerful spring (Novak 1987). Müller-Schwarze and Haggart (2005) described a modified safety device that reduces the chance of injury. Hancock traps (set on banks) and Bailey traps (set in shallow water) are suitcase-style traps that hold the beaver above water in a mesh cage until released (Baker and Hill 2003). Snares are inexpensive, easy to use, and can increase trapping efficiency because the area can be saturated with them; however, they suffer from increased risk of mortality from predation, suffocation, or drowning (Hill 1982).

Beavers can be marked with ear tags, neck collars, tail tags, and other devices (Novak 1987). Ear tags are problematic because of the beaver's small and thin ears, and neck collars are easily lost over the beaver's V-shaped neck and head. The tail can be marked with holes, notches, paint, or branding (Baker and Hill 2003). Tail-mounted radio transmitters can cause abrasions and have been known to get caught on underwater branches and cause drowning (Easter-Pilcher personal communication 2006). Transmitters implanted in the peritoneum have been used with some success (Davis et al. 1984, Gorsshkov et al. 1999). Passive integrated transponder (PIT) tags can be subcutaneously implanted and used to identify captured beavers or free-ranging animals by reading them with a scanner as beavers enter or exit burrows and lodges (Baker and Hill 2003). The longevity and effectiveness of marking techniques, as well as the trauma caused to beavers during and after marking, need to be considered when choosing a marking technique.

Transplanting populations

Transplanting beavers is an effective means of restoring beaver populations. Reintroductions across North America have helped to restore populations devastated by the early fur trade (Henderson 1960, Novak 1987, Olson and Hubert 1994). Reintroductions have traditionally been used to restore extirpated populations, to bolster low population numbers, and to expand current ranges (Deems and Pursley 1983). Increasingly, reintroductions are also used to restore beavers to ecologically degraded habitats (Apple 1985, McKinstry and Anderson 1999, McKinstry et al. 2001). When trapping from a source population, the entire colony (family group or mated adult pair) should be captured and transported together to the new site to ensure successful establishment of a breeding colony at the new site (Rutherford 1964). McKinstry and Anderson (2002) reported high losses from mortality and emigration when they released groups of unpaired beavers to restoration sites in Wyoming, and additional transplant operations were necessary to provide mates for unmated beavers that established territories. No kit or yearling age beavers attempted to build a dam or lodge, and all died or emigrated from the release site within six months. Livestock grazing must be managed prior to reintroductions to ensure adequate aquatic and riparian plant biomass for beaver summer food, and to permit sufficient growth of willows or other woody vegetation for winter food (Baker and Hill 2003). At ecologically damaged sites, aspen, willow, or cottonwood can be provisioned at the site to ensure adequate winter food and building materials until riparian vegetation develops from dam-building activity (Apple et al. 1985). In streams that are prone to flooding, initial dams built by reintroduced beavers may wash out. Construction of anchored dam bases made of large mesh wire has been effective in providing beavers a dam base to which they add plant material (Müller-Schwarze and Sun 2003).

Harvest management

Sustainable beaver harvest management requires information on population parameters such as juvenile recruitment, sex ratios, age of sexual maturity, pregnancy rates, and litter size (Hill 1982). Management plans should be implemented on a watershed scale due to the beaver's ability to disperse along watercourses to reach available suitable habitat (Olson and Hubert 1994). Where commercial beaver harvest is allowed, harvest quotas should be implemented to ensure that the population is not overharvested. For stable beaver populations, a sustainable harvest is probably about 20 to 25 percent (Payne 1984b).

Region 2 states employ various management strategies to regulate commercial harvest of beavers. Colorado is the only state in Region 2 without commercial beaver harvest, due to regulations prohibiting lethal trapping methods. Lethal trapping is selectively permitted for beavers to protect property, agriculture, or human health and safety. Beavers may be trapped without limit from October 30 to April 1 when permitted by the Colorado Division of Wildlife to control property damage, and a thirty-day exemption is allowed for authorized landowners to prevent livestock and crop damage (Colorado Division of Wildlife 2004). Trapping by licensed trappers is allowed statewide without limit in Kansas from November 12 to March 31 (Kansas Department of Wildlife and Parks 2004), in Nebraska from November 1 to March 31 (Nebraska Game and Parks Commission 2004), and in South Dakota from November 1 to March 31 (Huxoll 2003). Wyoming has designated several beaver trapping areas where beaver harvest is restricted by a quota ranging from 5 to 30 beavers per trapper. A limited number of trapping permits is issued for each area, and permitted trappers may harvest during only one of two trapping seasons from October 1 to December 31 and from January 1 to April 30 (Wyoming Game and Fish Department 2004). Outside of quota areas, beavers may be trapped during seasons without limit.

Beaver damage control

Control of damage caused by beavers is a common management concern. Removing beavers by either lethal or non-lethal means provides only short-term relief because the remaining beaver population can quickly grow and beavers are good dispersers. Localized kill trapping can be effective for population control (Deems and Pursley 1983, Peterson and Payne 1986, Collen and Gibson 2000, Higgins et al. 2000), but lethal methods are not always publicly acceptable. Transplanting nuisance beavers to other areas is frequently attempted (Olson and Hubert 1994, McKinstry and Anderson 2002). However, transplanting operations can be expensive and time-consuming, survival of transplanted beavers is likely to be poor unless the transplant is properly planned, and it may be difficult to find unoccupied habitat where beavers will not be considered undesirable. Incorporating principles of beaver ecology in development planning in beaver habitat can help to avoid conflicts with beavers, for example road designs with raised beds and stream crossings where a steep gradient discourages beavers from building dams (Munther 1983, Müller-Schwarze and Haggart 2003). Curtis and Jensen (2004) found that most beavers along roadsides in New York occurred in areas with more than 50 percent cover of woody vegetation, stream gradients of 3 percent or less, and streams less than 3 m wide. They suggested that these factors (or similar locally-derived data) can be used in planning roads along streams or at stream crossings to minimize conflicts with beavers.

Non-lethal damage control devices are emerging as the most effective long-term beaver damage control solution. These methods minimize impacts to beaver populations by allowing them to occupy suitable habitat, retaining the ecological benefits of beaver habitat modifications, while reducing or eliminating conflicts with human land uses. Beaver exclusion devices made of strong wire can prevent beavers from detecting flowing water that stimulates their dam-building response, preventing blocked culverts and irrigation structures (Munther 1983, Olson and Hubert 1994, Schulte and Müller-Schwarze 1999, Wilson and Ruff 1999). Water level control devices such as PVC pipe can be inserted into dams to limit flooding to acceptable levels (Lisle personal communication 2004). Wire mesh or decorative stone structures around desirable trees can prevent beaver cutting. Designs for these and other beaver control methods are provided by various conservation organizations (e.g., Beavers: Wetlands and Wildlife at http://www.beaversww.org/index.html). Jensen et al. (2001) describe devices for reducing beaver damage to roads from plugged culverts and flooding.

Public education programs

Beavers were severely reduced in the past due to human actions, and human attitudes about beavers remain a critical aspect of their conservation (Schulte personal communication 2006). Maintaining viable beaver populations and using beavers to promote ecosystem restoration require agency support and, sometimes, public cooperation, particularly when private lands and agricultural practices may be affected. Public education and information programs advancing the positive aspects of beavers could include information on the beaver's role as a keystone species, their benefits to fisheries, wildlife, water quality, and flood control, and non-lethal methods to control damage. State cooperative extension agencies often have useful educational materials about beavers, and many conservation groups provide a wealth of non-technical information and educational material through websites.

Information Needs

Improved techniques for accurately estimating populations are an important information need. All Region 2 state agencies report that detailed information on beaver populations would be a helpful tool for managing beaver fur harvest and damage problems.

Beaver management could be enhanced by more information on the key factors influencing population dynamics such as colony site longevity and the factors affecting habitat quality, mortality and fecundity, and dispersal patterns. Understanding beaver populations at landscape scales will require more information on metapopulation factors such as dispersal capabilities, and landscape features including human uses that enhance or interfere with colony movements.

Monitoring of transplanted populations is often overlooked. Information on survival statistics and factors affecting first-year survival of transplanted beavers would greatly improve the success of transplant operations.

Throughout Region 2, the primary conservation element facing managers is nuisance problems caused by beavers. Continued development of beaver damage control methods that allow beavers to remain on the landscape would provide a long-term management solution to beaver-human conflicts while conserving beaver populations and retaining the considerable ecological benefits that beavers provide. Better understanding of the beaver's ecological role in influencing the structure and function of Region 2 watersheds will also improve managers' use of beavers as a tool for restoring wetland and riparian functions.

There is an extensive body of scientific and management literature available on beaver biology and ecology. However, gaps in our existing knowledge of beavers have been identified. According to McKinstry et al. (2001), no studies have addressed the impact of removing beavers from western United States landscapes on wetland-dependent species. Factors affecting lodge site selection could be useful to managers identifying and protecting existing habitat (Dieter 1987); studies of these factors similar to Easter-Pilcher's (1987) work in northeastern Montana could be conducted in various Region 2 habitats to better understand the role of habitat in population regulation. In addition, since most beaver studies have been conducted from a biological rather than a hydrological perspective, more research is needed on the hydrological effects of dam size and distribution, changes in channel morphology, and flow dynamics at the dam and downstream (Gurnell 1998).

DEFINITIONS

Abundance – total number of beavers in a population at a given time.

Colony – a group of beavers occupying a single pond or group of ponds and cooperatively maintaining dams; typically consist of three to eight beavers comprising a mated pair with young of the year, and sometimes unmated subadults; colonies also sometimes consist of a mated pair without offspring or a single unmated adult; in large rivers that cannot sustain dams, beaver colonies consist of similar family groups.

Crepuscular – active at dawn or dusk.

Density – the total number of beavers per unit area in a population at a given time; because beavers inhabit linear waterways or shorelines, density is best expressed as animals per unit length of waterway or shoreline.

Epizootic – an infectious disease caused by microorganisms.

Home range – the total area occupied by an individual during a specified time interval; usually expressed as linear length of waterway or shoreline.

Population – the total number of beavers in a group with regular access to each other for breeding; beavers in Region 2 are typically distributed along linear waterways, and major watersheds are generally considered to be boundaries for populations; beavers probably function as metapopulations (group of subpopulations) both within watersheds and at larger regional scales.

Primary dispersal – a dispersal movement by a subadult beaver.

Secondary dispersal – a dispersal movement of an adult beaver.

Sink population – within a metapopulation, a satellite population that declines or becomes extirpated, especially during unfavorable years, and is dependent on immigration from core areas, or source populations, for existence over time.

Source population – within a metapopulation, a core population that tends to persist over time and may sustain outlying sink populations through emigration.

Stream gradient – the vertical drop of a stream divided by the horizontal distance, expressed as a percent.

References

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). Journal of Mammalogy 49:759-762.

Aleksiuk, M. 1970. The seasonal food regime of arctic beaver. Ecology 51:264-270.

Allen, A.W. 1983. Habitat suitability index models: Beaver. FWS/OBS-82/10.30. Revised. USDI Fish and Wildlife Service, Washington, D.C.

Apker, J. 2004. Statewide Terrestrial Biologist, Colorado Division of Wildlife, Denver, CO. Personal communication.

Apple, L.L. 1985. Riparian habitat restoration and beavers. Pages 489-490 *in* Riparian ecosystems and their management: Reconciling conflicting uses. USDA Forest Service General Technical Report RM-120. Fort Collins, CO.

Apple, L.L., B.H. Smith, J.D. Dunder, and B.W. Baker. 1985. The use of beavers for riparian/aquatic habitat restoration of cold desert, gully-cut stream systems in southwestern Wyoming. Pages 123-130 *in* G. Pilleri, editor. Investigations on beaver, volume 4. Brain Anatomy Institute, Berne, Switzerland.

Baker, A.B. 1889. Mammals of western Kansas. Transactions of the Kansas Academy of Sciences 11:56-58.

Baker, B.W. and B.S. Cade. 1995. Predicting biomass of beaver food from willow stem diameters. Journal of Range Management 48:322-326.

Baker, B.W., H.C. Ducharme, D.C.S. Mitchell, T.R. Stanley, and H.R. Peinetti. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. Ecological Applications 15:110-118.

Baker, B.W. and E.P. Hill. 2003. Beaver. Pages 288-310 *in* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. Wild mammals of North America: Biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, MD.

Balodis, M.M. 1994. Beaver populations of Latvia: History, development and management. Proceedings of the Latvian Academy of Sciences B 7/8:122-127.

Barnes, W.J. and E. Dibble. 1988. The effects of beaver in riverbank forest succession. Canadian Journal of Botany 66:40-44.

Basey, J.M. 1999. Foraging behavior of beavers (*Castor canadensis*), plant secondary compounds, and management concerns. Pages 129-146 *in* P.E. Busher and R. Dzieciolowski, editors. Beaver protection, management, and utilization in Europe and North America. Kluwer Academic and Plenum Publishers, New York, NY.

Bates, J.W. 1963. The effects of beaver on stream flow. Departmental Information Bulletin Number 63-13. Utah Division of Wildlife Resources, Salt Lake City, UT.

Bee, J.W., G.E. Glass, R.S. Hoffman, and R.R. Patterson. 1981. Mammals in Kansas. Public Education Series Number 7. University of Kansas, Lawrence, KS.

Belovsky, G.E. 1984. Summer diet optimization by beaver. American Midland Naturalist 111:209-222.

Bergerud, A.T. and D.R. Miller. 1977. Population dynamics of Newfoundland beaver. Canadian Journal of Zoology 55:1480-1492.

Beschta, R.L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications 13:1295-1309.

Bhat, M.G., R.G. Huffaker, and S.M. Lenhart. 1993. Controlling forest damage by dispersive beaver populations: Centralized optimal management strategy. Ecological Applications 3:518-530.

Bishir, J., R.A. Lancia, and H.E. Hodgdon. 1983. Beaver family organization: Its implications for colony size. Pages 105-113 *in* G. Pilleri, editor. Investigations on beavers. Volume 4, Brain Anatomy Institute, Berne, Switzerland.

Boyce, M.S. 1981. Habitat ecology of an unexploited population of beaver in interior Alaska. Pages 55-86 *in* J.A. Chapman and D. Pursley, editors. Proceedings of the worldwide furbearer conference, Frostburg, MD.

Brady, C.A. and G.E. Svendson. 1981. Social behaviour in a family of beaver, *Castor canadensis*. Biology of Behaviour 6:99-114.

Brenner, F.J. 1967. Spatial and energy requirements of beaver. Ohio Journal of Science 67:242-246.

Buech, R.R. 1985. Beaver in water impoundments: understanding a problem of water-level management. Pages 95-105 *in* M.D. Knighton, editor. Water impoundments for wildlife: a habitat management workshop. USDA Forest Service General Technical Report NC-100. St. Paul, MN.

Buech, R.R., D.J. Rugg, and N.L. Miller. 1989. Temperature in beaver lodges and bank dens in a near-boreal environment. Canadian Journal of Zoology 67:1061-1066.

Buskirk, S.W. 2000. The conservation status of New World mustelids. Pages 41-52 *in* H.I. Griffiths, editor. Mustelids in a modern world: Management and conservation aspects of small carnivore: human interactions. Backhuys, Leiden, Netherlands.

Butler, R.G. and L.A. Butler. 1979. Toward a functional interpretation of scent marking in the beaver (*Castor canadensis*). Behavioral and Neural Biology 26:442-454.

Call, M.W. 1966. Beaver pond ecology and beaver-trout relationships in southeastern Wyoming. University of Wyoming and Wyoming Game and Fish Commission, Laramie, WY.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, MA.

Chamberlain, T.C. 1897. The method of multiple working hypotheses. Journal of Geology 5:837-848. Reprinted in Science 148:754-759.

Cochran, M.E. and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs 62:345-364.

Cockrum, E.L. 1952. Mammals of Kansas. University of Kansas Museum of Natural History Publications 7:1-303.

Coles, R.W. 1970. Pharyngeal and lingual adaptations in the beaver. Journal of Mammalogy 51:424-425.

Collen, P. and R.J. Gibson. 2000. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish - a review. Reviews in Fish Biology and Fisheries 10:439-461.

Collins, T. 1993. The role of beaver in riparian habitat management. Habitat Extension Bulletin Number 38. Wyoming Game and Fish Department, Cheyenne, WY.

Colorado Division of Wildlife. 2004. Colorado Division of Wildlife website. Available online at: http://wildlife.state.co.us [Accessed August 26, 2004].

Courcelles, R. and R. Nault. 1983. Beaver programs in the James Bay area, Quebec, Canada. Acta Zoologic Fennica 174:129-131.

Crowe, D.M. 1986. Furbearers of Wyoming. Wyoming Game and Fish Department, Cheyenne, WY.

Cuplin, P. 1985. Riparian area inventory and monitoring using large scale color infrared photography. Pages 69-71 *in* Riparian ecosystems and their management: Reconciling conflicting uses. USDA Forest Service General Technical Report RM-120. Fort Collins, CO.

Currier, A., W.D. Kitts, and I. McT. Cowan. 1960. Cellulose digestion in the beaver (*Castor canadensis*). Canadian Journal of Zoology 38:1109-1116.

Curry-Lindahl, K. 1967. The beaver, *Castor fiber* Linnaeus, 1758 *in* Sweden - extermination and reappearance. Acta Theriologica 12:1-15.

Curtis, P.D. and P.G. Jensen. 2004. Habitat features affecting beaver occupancy along roadsides in New York State. Journal of Wildlife Management 68:278-287.

Davis, J.R., A.F. Von Recum, D.D. Smith, and D.C. Guynn. 1984. Implantable telemetry in beaver. Wildlife Society Bulletin 12:322-324.

Deems, E.F., Jr., and D. Pursley, editors. 1983. North American furbearers: A contemporary reference. International Association of Fish and Wildlife Agencies and Maryland Department of Natural Resources - Wildlife Administration, Washington, D.C.

Denney, R.N. 1952. A summary of North American beaver management, 1946-1948. Current Report Number 28. Colorado Game and Fish Department (now Colorado Division of Wildlife), Denver, CO.

Dickinson, N.R. 1971. Aerial photographs as an aid in beaver management. New York Fish and Game Journal 18: 57-61.

Dieter, C.D. 1987. Habitat use by beaver along the Big Sioux River. MS Thesis. South Dakota State University, Brookings, SD.

Doboszynska, T. and W. Zurowski. 1983. Reproduction of the European beaver. Acta Zoologica Fennica 174:123-126.

Easter-Pilcher, A. 1990. Cache size as an index to beaver colony size in northwestern Montana. Wildlife Society Bulletin 18:110-113.

Easter-Pilcher, A. 2006. Associate Professor of Biology, Dept. of Environmental Sciences, University of Montana-Western, Dillon, MT. Personal communication.

Easter-Pilcher, A.L. 1987. Forage utilization, habitat selection and population indices of beaver in northwestern Montana. M.S. Thesis. University of Montana, Missoula, MT. 88 pp.

Elliott, J.G., A.C. Gellis, and S.B. Aby. 1999. Evolution of arroyos: incised channels of the southwestern United States. Pages 153-185 *in* S.E. Darby and A. Simon, editors. Incised river channels: Processes, forms, engineering and management. John Wiley, New York, NY.

Emlen, J.M. 1973. Ecology: an evolutionary approach. Addison-Wesley Publishing Co., Inc., Reading, MA.

Fitzgerald, J.P., C.A. Meaney, and D.M. Armstrong, editors. 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado, Niwot, CO.

Fryxell, J.M. 2001. Habitat suitability and source-sink dynamics of beavers. Journal of Animal Ecology 70:310-316.

Gallant, D., C.H. Bérubé, E. Tremblay, and L. Vasseur. 2004. An extensive study of the foraging ecology of beavers (*Castor canadensis*) in relation to habitat quality. Canadian Journal of Zoology 82:922-933.

Gorshkov, Y.A., A.L. Easter-Pilcher, B.K. Pilcher, and D.Y. Gorshkov. 1999. Ecological restoration by harnessing the work of beavers. In P.P.E. Busher and R. Dzieciolowski, editors. Beaver protection, management, and utilization in Europe and North America. Kluwer Academic and Plenum Publishers, New York, NY.

Grasse, J.E. and E.F. Putnam. 1955. Beaver management and ecology in Wyoming. Federal Aid in Wildlife Restoration Project Bulletin Number 6. Wyoming Game and Fish Commission, Cheyenne, WY.

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

Hack, M. 2006. Head of Research Analysis and Inventory Section, Nebraska Game and Parks Commission, Lincoln, NE. Personal communication.

Hair, J.D., G.T. Hepp, L.M. Luckett, K.P. Reese, and D.K. Woodward. 1979. Beaver pond ecosystems and their relationship to multi-use natural resources management. USDA Forest Service General Technical Report WO-12:80-92.

Härkönen, S. 1999. Management of the North American beaver (*Castor canadensis*) on the South-Savo Game Management District, Finland (1983-1997). Pages 7-14 *in* P.E. Busher and R. Dzieciolowski, editors. Beaver protection, management, and utilization in Europe and North America. Kluwer Academic and Plenum Publishers, New York, NY.

Hay, K.G. 1955. Development of a beaver census method applicable to mountain terrain in Colorado. MS Thesis. Colorado State University, Fort Collins, CO.

Hayward, G.H., et al. 2001. Draft process to evaluate species and population viability in forest planning and plan implementation in the Rocky Mountain Region. USDA Forest Service, Lakewood, CO.

Henderson, F.R. 1960. Beaver in Kansas. State Biological Survey and Museum of Natural History Miscellaneous Publication Number 26. University of Kansas, Lawrence, KS.

Henry, D.B. and T.A. Bookout. 1969. Productivity of beavers in northeastern Ohio. Journal of Wildlife Management 33:927-932.

Hensley, A.L. and B.C. Fox. 1948. Experiments on the management of Colorado River beaver. California Fish and Game 43:115.

Hibbard, E.A. 1958. Movements of beaver transplanted in North Dakota. Journal of Wildlife Management 22:209-211.

Higgins, K.E., E.D. Stukel, J.M. Goulet, and D.C. Backlund. 2000. Wild mammals of South Dakota. South Dakota Department of Game, Fish, and Parks, Pierre, SD.

Hilborn, R. and M. Mangel. 1997. The ecological detective: Confronting models with data. Princeton University Press, Princeton, NJ.

Hill, E.P. 1982. Pages 256-281 *in* J.A. Chapman and G.A. Feldhamer, editors. Wild mammals of North America: Biology, management, and economics. Johns Hopkins University Press, Baltimore, MD.

Howard, R.J. and J.S. Larson. 1985. A stream habitat classification system for beaver. Journal of Wildlife Management 49:19-25.

Huxoll, C. 2003. South Dakota Game Report Number 2003-11. South Dakota Department of Game, Fish and Parks, Pierre, SD.

Irving, L. and M.D. Orr. 1935. The diving habits of the beaver. Science 82:569.

Jenkins, S.H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Jenkins, S.H. and P.E. Busher. 1979. *Castor canadensis*. American Society of Mammalogists Mammalian Species 120:1-8.

Jensen, P.G., P.D. Curtis, M.E. Lehnert, and D.L. Hamelin. 2001. Habitat and structural features influencing beaver interference with highway culverts. Wildlife Society Bulletin 29:654-664.

Johnston, C.A. and R.J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landscape Ecology 1:47-57.

Jones, J.K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas Museum of Natural History Publications 16:1-356.

Kansas Department of Wildlife and Parks. 2004. Kansas Department of Wildlife and Parks website. Available online at: http://www.kdwp.state.ks.us [Accessed August 26, 2004].

Kay, C.E. 1994. The impact of native ungulates and beaver on riparian communities in the Intermountain West. Natural Resources and Environmental Issues 1:23-44.

Kiesow, A. 2004. Terrestrial Biologist, South Dakota Game, Fish, and Parks Commission, Pierre, SD. Personal communication.

Knudsen, G.J. and J.B. Hale. 1965. Movements of transplanted beaver in Wisconsin. Journal of Wildlife Management 29:685-688.

Kondolf, G.M., G.F. Cada, M.J. Sale, and T. Felando. 1991. Distribution and stability of potential salmonid spawning gravels in steep boulder-bed streams of the Eastern Sierra Nevada. Transactions of the American Fisheries Society 120:177-186.

Larson, J.S. 1967. Age structure and sexual maturity within a western Maryland beaver (*Castor canadensis*) population. Journal of Mammalogy 48:408-413.

Larson, J.S. and J.R. Gunson. 1983. Status of the beaver in North America. Acta Zoologica Fennica 174:91-93.

Leege, T.A. 1968. Natural movements of beavers in southeastern Idaho. Journal of Wildlife Management 32:973-976.

Leege, T.A. and R.M. Williams. 1967. Beaver productivity in Idaho. Journal of Wildlife Management 31:326-332.

Lisle, S. 2004. Wildlife Consultant, Old Town, Maine. Personal communication.

Maret, J.J., M. Parker, and T.E. Fannin. 1987. The effect of beaver ponds on the non-point source water quality of a stream in southwestern Wyoming. Water Resources 21:263-268.

Martin, P.R. 1977. The effect of altered streamflow on furbearing mammals of the Yellowstone River Basin, Montana. Technical Report Number 6. Water Resources Division, Montana Department of Natural Resources and Conservation, Helena, MT.

McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current ornithology. Volume 10. Plenum Press, New York, NY.

McDowell, D.M. and R.J. Naiman. 1986. Structure and function of a benthic invertebrate community as influenced by beaver. Oecologia (Berlin) 68:481-489.

McGinley, M.A. and T.G. Whitham. 1985. Central place foraging by beavers (*Castor canadensis*): A test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia 66:558-562.

McKean, T. 1982. Cardiovascular adjustments to laboratory diving in beavers and nutria. American Journal of Physiology 242:R434-R440.

McKinstry, M.C. and S.H. Anderson. 1999. Attitudes of private- and public-land managers in Wyoming, USA, toward beaver. Environmental Management 23:95-101.

McKinstry, M.C. and S.H. Anderson. 2002. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. Canadian Field-Naturalist 116:60-68.

McKinstry, M.C., P. Caffrey, and S.H. Anderson. 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. Journal of the American Water Resources Association 37:1571-1577.

McKinstry, M.C., R.R. Karhu, and S.H. Anderson. 1997. Use of active beaver, *Castor canadensis*, lodges by muskrats, *Ondatra zibethicus*, in Wyoming. Canadian Field-Naturalist 111:310-311.

Medin, D.E. and W.P. Clary. 1991. Small mammals of a beaver pond ecosystem and adjacent riparian habitat in Idaho. USDA Forest Service Research Paper INT-445. Intermountain Research Station, Ogden, UT.

Mills, L.S., M.E. Soule, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience 43:219-223.

Morris, W.F. and D.F. Doak. 2002. Quantitative conservation biology. Sinauer Associates, Sunderland, MA.

Müller-Schwarze, D. and D.P. Haggart. 2005. A better beaver trap-new safety device for live traps. Wildlife Society Bulletin 33:359-361.

Müller-Schwarze, D. and S. Heckman. 1980. The social role of scent marking in beaver (*Castor canadensis*). Journal of Chemical Ecology 6:81-95.

Müller-Schwarze, D. and L. Sun. 2003. The beaver: Natural history of a wetlands engineer. Cornell University Press, Ithaca, NY.

Munther, G.L. 1982. Beaver management in grazed riparian ecosystems. Pages 234-241 *in* J. M. Peek and P. D. Dalke, editors. Wildlife livestock relationships symposium: Proceedings 10. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, ID.

Munther, G.L. 1983. Integration of beaver into forest management. Proceedings of the Eighteenth Annual Meeting of the American Fisheries Society, Laramie, WY.

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

NatureServe Explorer: An online encyclopedia of life [web application]. 2005. Arlington, VA: NatureServe. Available online at: http://www.natureserve.org/explorer [Accessed September 29, 2005].

Nebraska Game and Parks Commission. 2004. Nebraska Game and Parks Commission website. Available online at: http://www.ngpc.state.ne.us [Accessed August 26, 2004].

Nolet, B.A., A. Hoekstra, and M.M. Ottenheim. 1994. Selective foraging on woody species by the beaver, *Castor fiber*, and its impact on a riparian willow forest. Biological Conservation 70:117-128.

Novak, M. 1987. Beaver. Pages 282-313 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Olson, R. and W.A. Hubert. 1994. Beaver: Water resources and riparian habitat manager. University of Wyoming Press, Laramie, WY.

Osborn, D.J. 1953. Age classes, reproduction, and sex ratios of Wyoming beaver. Journal of Mammalogy 34:27-44.

Osmundson, C.L. and S.W. Buskirk. 1993. Size of food caches as a predictor of beaver colony size. Wildlife Society Bulletin 21:64-69.

Parker, M., F. Wood, Jr., B.H. Smith, and R.G. Elder. 1985. Erosional downcutting in lower order riparian ecosystems: have historical changes been caused by removal of beaver? Pages 35-38 *in* Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service General Technical Report RM-120. Fort Collins, CO.

Patric, E.F. and W.L. Webb. 1960. An evaluation of three age determination criteria in live beaver. Journal of Wildlife Management 24:37-44.

Payne, N.F. 1984a. Population dynamics of beaver in North America. Acta Zoologica Fennica 172:263-266.

Payne, N.F. 1984b. Mortality rates of beaver in Newfoundland. Journal of Wildlife Management 48:117-126.

Payne, N.F. 1984c. Reproductive rates of beaver in Newfoundland. Journal of Wildlife Management 48:912-917.

Peek, M. 2004. Furbearer Biologist, Kansas Department of Wildlife and Parks, Topeka, KS. Personal communication.

Peterson, R.P. and N.F. Payne. 1986. Productivity, size, age, and sex structure of nuisance beaver colonies in Wisconsin. Journal of Wildlife Management 50:265-268.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213-218.

Platt, J.R. 1964. Strong inference. Science 146:347-353.

Polechla, P.J. 1989. More evidence of a commensal relationship between the river otter and the beaver. Pages 217-236 *in* C.J. Amlaner, editor. Biotelemetry X: Proceedings of the tenth international symposium on biotelemetry. University of Arkansas Press, Fayetteville, AR.

Prichard, D. 1998. Riparian area management, a user guide to assessing proper functioning condition and the supporting science for lotic areas. TR-1735-15. U.S. Department of the Interior, Bureau of Land Management, Washington, D.C.

Provost, E.E. 1958. Studies on reproduction and population dynamics in beaver. Ph.D. Dissertation. Washington State University, Pullman, WA.

Reid, D.G., T.E. Code, A.C. H. Reid, and S.M. Herrero. 1994. Spacing, movements, and habitat selection of the river otter in boreal Alberta. Canadian Journal of Zoology 72:1314-1324.

Retzer, J.L., H.M. Swope, J.D. Remington, and W.H. Rutherford. 1956. Suitability of physical factors for beaver management in the Rocky Mountains of Colorado. Technical Bulletin 2. Colorado Department of Game and Fish (now Colorado Division of Wildlife), Denver, CO.

Ringelman, J.K. 1991. Managing beaver to benefit waterfowl. Fish and Wildlife Leaflet 13.4.7. U.S. Fish and Wildlife Service, Washington, D.C.

Robel, R.J. and L.B. Fox. 1993. Comparison of aerial and ground survey techniques to determine beaver colony densities in Kansas. Southwestern Naturalist 38:357-361.

Rosell, F., O. Bozsér, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35:248-276.

Rothwell, R. 2004. Supervisor of Biological Services, Wyoming Game and Fish Department. Cheyenne, WY. Personal communication.

Rue, L.E., III. 1964. The world of the beaver. J. B. Lippincott Company, Philadelphia, PA.

Rutherford, W.H. 1964. The beaver in Colorado: Its biology, ecology, management, and economics. Colorado Game, Fish, and Parks Department Technical Publication 17:1-49.

Schulte, B.A. 2006. Associate Professor, Dept. of Biology, Georgia Southern University, Statesboro, GA. Personal communication.

Schulte, B.A. and D. Müller-Schwarze. 1999. Understanding North American beaver behavior as an aid to management. Pages 109-128 *in* P.E. Busher and R. Dzieciolowski, editors. Beaver protection, management, and utilization in Europe and North America. Kluwer Academic and Plenum Publishers, New York, NY.

Schulte, B.A., D. Müller-Schwarze, and L. Sun. 1995. Using anal gland secretion to determine sex in beaver. Journal of Wildlife Management 59:614-618.

Slough, B.G. and R.M.F.S Sadleir. 1977. A land capability classification system for beaver (*Castor canadensis* Kuhl). Canadian Journal of Zoology 55:1324-1335.

Smith, B.H. 1982. Livestock-riparian-fisheries interrelationships; or, functional applications of adaptation for personal survival. Proceedings of the Seventeenth Annual Meeting, Colorado-Wyoming Chapter, American Fisheries Society, Fort Collins, CO.

Southwestern Wyoming Water Quality Planning Association. 1978. Clean water report for southwestern Wyoming. CH2M-Hill Inc., Denver, CO.

Stack, W.R. and R.L. Beschta. 1989. Factors influencing pool morphology in Oregon coastal streams. Pages 401-411 *in* Headwaters hydrology. American Water Resources Association Hydrology Symposium, June 23-27, Missoula, MT.

Sun, L., D. Müller-Schwarze, and B. Schulte. 2000. Dispersal pattern and effective population size of the beaver. Canadian Journal of Zoology 78:393-398.

Swanston, D.N. 1991. Natural processes. Pages 139-179 *in* W.R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19. Bethesda, MD.

Swenson, J.E., S.J. Knapp, P.R. Martin, and T.C. Hinz. 1983. Reliability of aerial cache surveys to monitor beaver population trends on prairie rivers in Montana. Journal of Wildlife Management 47:697-703.

Thompson, W.L., G.C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, New York, NY.

Townsend, J.E. 1953. Beaver ecology in western Montana with special reference to movements. Journal of Mammalogy 34:459-470.

Vacirca, R. 2005. Fisheries Biologist, USDA Forest Service, Region 2, Lakewood, CO. Personal communication.

Van Deelen, T.R. and D.H. Pletscher. 1996. Dispersal characteristics of two-year-old beavers, *Castor canadensis*, in western Montana. Canadian Field-Naturalist 110:318-321.

Vanden Berge, R.J. and P.A. Vohs, Jr. 1977. Population status of beaver on the free-running Missouri River in southeastern South Dakota. Proceedings of the South Dakota Academy of Science 56:230-236.

Wall, R. 1939. Seventh biennial report of Forestry, Fish and Game Commission of the State of Kansas, for the period ending June 30, 1938. Kansas Forestry, Fish and Game Commission (now Kansas Department of Wildlife and Parks), Topeka, KS.

Welch, D.K., R.J. Robel, and L.B. Fox. 1993. Age structure and reproductive activity in a Kansas beaver population. Transactions of the Kansas Academy of Science 96:186-195.

Wessels, T. 2001. Abandonment: on beaver ecology and recovery. Wild Earth 11:62-67.

Wigley, T.B., T.H. Roberts, and D.H. Arner. 1983. Reproductive characteristics of beaver in Mississippi. Journal of Wildlife Management 47:1171-1177.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.

Wilson, D.E. and S. Ruff, editors. 1999. The Smithsonian book of North American mammals. Smithsonian Institution Press in association with the American Society of Mammalogists, Washington, D.C.

Wilsson, L. 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). Viltrevy 8:115-226.

Wilsson, M.F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

Wyoming Game and Fish Department. 2004. Wyoming Game and Fish Department website. Available online at: http://gf.state.wy.us [Accessed August 26, 2004].

Yeager, L.E. and W.H. Rutherford. 1957. An ecological basis for beaver management in the Rocky Mountain Region. Transactions of the North American Wildlife and Natural Resources Conference 22:269-300.

Appendix

Population Matrix Model for the Beaver

Life cycle graph and model development

Life history characteristics compiled from various references cited in the Breeding Biology sections (see especially Baker and Hill 2003, Payne 1984a and 1984b, and Novak 1987) provided the basis for a nine-stage life cycle graph (**Figure A1**) and a matrix population analysis for a birth-pulse population with a one-year census interval and a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001) for beavers. The model has three kinds of input terms: P_i describing survival rates, m_i describing fertilities, and B_i describing probability of breeding (**Table A1**).

Table A1 shows the input matrix of vital rates corresponding to the beaver life cycle graph (**Figure A1**). **Figure A2a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure A2b** gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the offspring number used was half the litter size, assuming a 1:1 sex ratio at birth. Note also that the fertility terms (F_i) in the top row of

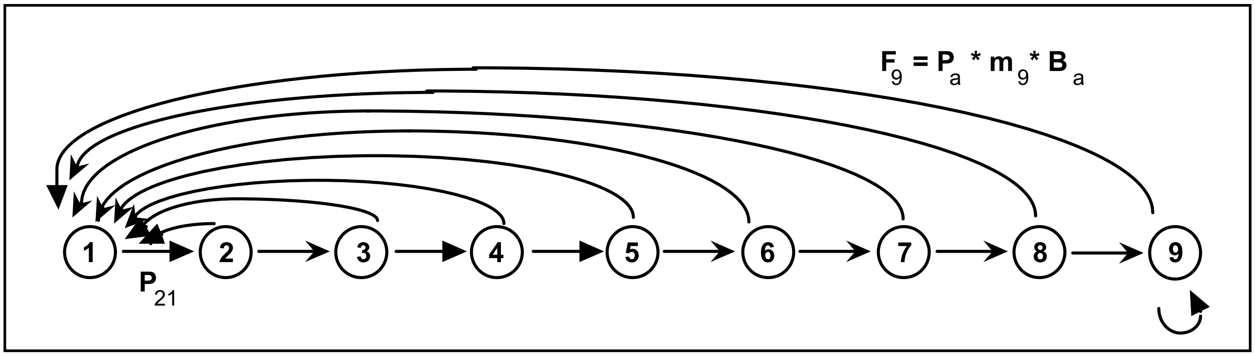

Figure A1. Life cycle graph for the beaver, consisting of circular nodes, describing stages in the life cycle and arcs, describing the vital rates (transitions between stages). The horizontal arcs are survival transitions (e.g., first-year survival, P_{21} = 0.58). The self-loop from Node 9 to itself describes survival of the mixed-age stage of oldest females. That is, Stages 1 to 8 are age-specific (first-year, second-year etc.), while the final node is a mixed-age stage. The remaining arcs, pointing back to Node 1, describe fertility (e.g., $F_9 = P_a * m_9 * Ba$). The two symbolic values are illustrative examples. The full sets of symbolic and numeric values for the arcs are shown in **Figure A2a** and **Figure A2b**.

Table A1. Parameter values for the component terms (P_i, B_i and m_i) that make up the vital rates in the projection matrix for the beaver.

Parameter	Numeric value	Definition
m_2	1.55	Number of female offspring produced by a second-year female
m_3	1.8	Number of female offspring produced by a third-year female
m_4 to m_6	1.95	Number of female offspring produced by a "young adult" female
m_7 & m_8	2.1	Number of female offspring produced by an "older adult" female
m_9	1.9	Number of female offspring produced by oldest females
B_2	0.27	Probability of breeding in the second year
B_3	0.65	Probability of breeding in the third year
B_4	0.78	Probability of breeding in the fourth year
B_a	0.87	Probability of breeding as an "older adult"
P_{21}	0.58	First-year survival rate
P_{32}	0.42	Second-year survival rate
P_{43}	0.71	Third-year survival rate
P_a	0.87	Annual survival rate of "adult" females

Stage	1	2	3	4	5	6	7	8	9
1		$P_{32}*m_2*B_2$	$P_{43}*m_3*B_3$	$P_a*m_4*B_4$	$P_a*m_5*B_a$	$P_a*m_6*B_a$	$P_a*m_7*B_a$	$P_a*m_8*B_a$	$P_a*m_9*B_a$
2	P_{21}								
3		P_{32}							
4			P_{43}						
5				P_a					
6					P_a				
7						P_a			
8							P_a		
9								P_a	P_a

Figure A2a. Symbolic values for the matrix cells. The input matrix of vital rates, A (with cells a_{ij}) corresponding to the beaver life cycle graph (**Figure A1**). The top row is fertility with compound terms describing probability of breeding (B_i), survival of the mother (P_i) and offspring production (m_i). Note that the matrix is not purely age-classified because of a multi-age stage (No. 9) denoted by the self-loop term in the bottom right corner.

Stage	1	2	3	4	5	6	7	8	9
1		0.176	0.831	1.08	1.205	1.205	1.297	1.297	1.174
2	0.58								
3		0.42							
4			0.71						
5				0.71					
6					0.71				
7						0.71			
8							0.71		
9								0.71	0.71

Figure A2b. Numeric values. The input matrix of vital rates, A (with cells a_{ij}) corresponding to the beaver life cycle graph (**Figure A1)**.

the matrix include a term for offspring production (m_i) as well as a term for the survival of the mother (P_i) from the census (just after the breeding season) to the next birth pulse almost a year later, plus a term (B_i) for probability of breeding.

The population growth rate (λ) was 1.001 based on the estimated vital rates used for the matrix; some rates were adjusted upward slightly from the published estimates to yield a deterministic λ slightly greater than 1. Although this suggests a stationary population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

Sensitivity is the effect on λ of an absolute change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, A [**Figure A2**]). Sensitivity analysis provides several kinds of useful information (Caswell 2001). First, sensitivities show how important a given vital rate is to λ and, by inference, fitness. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to a paucity of data, but it could also result from inappropriate or biased estimation techniques or other errors of analysis. To improve the accuracy of population models, biologists should concentrate on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever these can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing the population growth rate.

Figure A3 shows the "possible sensitivities only" matrix for this analysis. In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor

Stage	1	2	3	4	5	6	7	8	9
1		0.109	0.046	0.032	0.023	0.016	0.012	0.008	0.02
2	0.323								
3		0.401							
4			0.184						
5				0.135					
6					0.096				
7						0.069			
8							0.048		
9								0.033	0.08

Figure A3. Possible sensitivities only matrix, S_p (remainder of matrix is zeros). The three transitions to which λ of the beaver is most sensitive are highlighted: survival through the first three years (Cells s_{21} to s_{43}).

that changes the annual survival rate of Stage 4 females is likely to cause similar changes in the survival rates of other adult female age classes. Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the sensitivity of λ to changes in second-year survival (0.401; 24 percent of total) and first-year survival (0.323; 20 percent of total) are considerably larger than to changes in other rates. The summed sensitivities of λ to changes in "adult" survival rates was 0.64 (39 percent of the total sensitivity). Beavers show less sensitivity to changes in fertility (the first row of the matrix in **Figure A3**, 10 percent of total). The major conclusion from the sensitivity analysis is that enhancement of early survival is the key to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For example, a change of 0.5 in survival may be highly significant to population viability (e.g., a change from 90 to 40 percent). However, a change of 0.5 in fertility may be a very small proportional change (e.g., a change in litter size from 3.5 to 4.0). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. The elasticities have the useful property of summing to 1.0.

The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of fertility (F_i) and survival (P_i) for a given species.

Elasticities for the beaver are shown in **Figure A4**. λ was most elastic to changes in first-year survival, followed successively by survival at subsequent ages. Overall, survival transitions accounted for approximately 81 percent of the total elasticity of λ to changes in the vital rates. The survival rates are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The stable stage distribution (SSD; **Table A2**) describes the proportion of each stage (or age-class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary, or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. At the time of the post-breeding annual census (just after the end of the breeding season), young of the year represent 41 percent of the population, with yearling prebreeders representing a further 24 percent of the population.

Reproductive values (**Table A3**) can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first (newborn) stage. The reproductive value of the first stage is always 1.0. A female individual in any of the breeding-age

Stage	1	2	3	4	5	6	7	8	9
1		0.019	0.038	0.035	0.028	0.02	0.015	0.011	0.023
2	0.187								
3		0.168							
4			0.131						
5				0.096					
6					0.068				
7						0.049			
8							0.034		
9								0.023	0.057

Figure A4. Elasticity matrix, E (remainder of matrix is zeros). λ for the beaver is most elastic to changes in survival through the first three years (Cells e_{21} to e_{43}).

Table A2. Stable stage distribution (SSD, right eigenvector). At the census, 24 percent of the population should be young of the year. Approximately 10 percent will be yearlings, and the remainder will be older females.

Stage	Description	Proportion
1	First-year females	0.414
2	Second-year females	0.240
3	Third-year females	0.101
4	Fourth-year females	0.071
5	Fifth-year females	0.051
6	Sixth-year females	0.036
7	Seventh-year females	0.025
8	Eighth-year females	0.018
9	Oldest females	0.044

Table A3. Reproductive values for females. Reproductive values can be thought of as describing the "value" of a stage as a seed for population growth, relative to that of the first (newborn) stage, which is always defined to have the value 1.0.

Stage	Description	Proportion
1	First-year females	0.414
2	Second-year females	0.240
3	Third-year females	0.101
4	Fourth-year females	0.071
5	Fifth-year females	0.051
6	Sixth-year females	0.036
7	Seventh-year females	0.025
8	Eighth-year females	0.018
9	Oldest females	0.044

stages (3 through 9) is "worth" approximately four female newborns (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The cohort generation time for beavers is 5.4 years (SD = 3.0 years).

Stochastic model

We conducted a stochastic matrix analysis for the beaver. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (Table A4). Under Variant 1, we altered the offspring production

Table A4. Summary of three variants of stochastic projections for beaver. Each variant consisted of 100 runs, each of which ran for 2,000 annual census intervals. Stochastic vital rates were selected from a beta distribution with mean at the deterministic value and SD of 1/4 or 1/8 of that deterministic mean.

	Variant 1	Variant 2	Variant 3
Input factors:			
Affected cells	F_i	P_{21} and P_{32}	P_{21} and P_{32}
S.D. of random normal distribution	1/4	1/4	1/8
Output values:			
Deterministic λ	1.001	1.001	1.001
# Extinctions / 100 trials	2	83	1
Mean extinction time	N.a.	1,185	1,514
# Declines / # surviving populations	62/98	16/17	80/99
Mean ending population size	28,803	4,810	15,450
Standard deviation	76,777	17,099	54,894
Median ending population size	4,155	167	1,890
Log λ_s	-0.0005	-0.006	-0.0009
λ_s	1.000	0.994	0.997
Percent reduction in λ	0.19	0.72	0.24

terms (m_i). Under Variants 2 and 3, we varied the survival of the first two age-classes (P_{21} and P_{32}). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) under the deterministic model.

Beginning at the SSD helps to avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of running each of 100 replicate populations for 2,000 annual cycles, from a starting size of 10,000. We varied the amount of fluctuation by varying the standard deviation of the beta distribution from which the stochastic vital rates were selected. The beta distribution has the useful property of existing in the interval zero to one, thereby avoiding problems of impossible parameter values (<0 or >1) or altered mean and variance (as when using a truncated normal distribution). The default value was a standard deviation of 1/4 of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate] a_{ij} under the deterministic analysis).

The stochastic model (**Table A4**) produced two major results. First, altering the survival rates had a much more dramatic effect on λ than altering the fertilities. For example, under the varied fertilities of Variant 1, the median ending size was 4,155 with two pseudoextinctions and 62 populations declining from their initial size. In contrast, the same degree of variation acting on survival under Variant 2 resulted in a median ending size of only 1,890, with one population going pseudoextinct, and 80 populations declining.

Second, large-effect stochasticity has a negative effect on population dynamics, at least when it impacts transitions to which λ is highly sensitive. The negative effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size.

Under the survival Variant 3 with a high degree of stochasticity (SD = 1/4 of the mean), 83 out of 100 trials of stochastic projection went to pseudoextinction with all but one of the surviving populations declining in size, and a median size for the surviving populations of just 167. Variant 3 shows that the magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Increasing the magnitude of fluctuation increased the severity of the negative impacts – the number of pseudoextinctions went from 1 to 83. These differences in the effects of stochastic variation are predictable from the sensitivities and elasticities. λ was much more sensitive to changes in first- and second-year survival, P_{21} and P_{32}, than it was to changes in the entire set of fertilities, F_i. These results suggest that beaver populations are relatively tolerant to stochastic fluctuations in offspring production (due, for example, to climatic variation or density-dependent fertility) but more vulnerable to variations in the survival of prebreeding individuals.

Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual survival), with consequent detrimental effects on population dynamics. Further, in the case of high sensitivity of λ to changes in first-year survival, selection may be relatively ineffective in reducing variability that surely results from a host of biotic and abiotic factors.

Refining the models

Clearly, the better the data on early survival rates, the more accurate the resulting analysis. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would incorporate forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

References

Baker, B.W. and E.P. Hill. 2003. Beaver. Pages 288-310 *in* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman, editors. Wild mammals of North America: Biology, management, and conservation. Second edition. Johns Hopkins University Press, Baltimore, MD.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, MA.

Cochran, M.E. and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs 62:345-364.

McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current ornithology. Volume 10. Plenum Press, New York, NY.

Novak, M. 1987. Beaver. Pages 282-313 *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Payne, N.F. 1984a. Mortality rates of beaver in Newfoundland. Journal of Wildlife Management 48:117-126.

Payne, N.F. 1984b. Reproductive rates of beaver in Newfoundland. Journal of Wildlife Management 48:912-917.

Pfister, C.A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213-218.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.