

THE IMPORTANCE OF BEAVER TO WETLAND HABITATS AND WATERFOWL IN WYOMING¹

Mark C. McKinstry, Paul Caffrey, and Stanley H. Anderson²

ABSTRACT: Beaver (*Castor canadensis*) are habitat-modifying keystone species, and their activities broadly influence many other plants and animals. Beaver are especially important to waterfowl in the western U.S. where riparian and wetland habitats comprise less than 2 percent of the landscape yet provide habitat for greater than 80 percent of wildlife species. Wyoming is currently ranked sixth of the 50 states in the size of its breeding waterfowl population, and beaver ponds may play a significant role in providing habitat for these birds. The objectives of this research were to: (1) identify streams in Wyoming where beaver are currently present, extirpated, or used to manage riparian habitat; (2) identify areas where beaver could be relocated to create wetlands and improve riparian habitat; (3) compare wetland surface areas between areas that have beaver with those that did not; and (4) compare waterfowl numbers in areas with and without beaver. Using a survey of 125 land managers in Wyoming, we found that beaver have been removed from 23 percent (6,497 km) of the streams for which managers had direct knowledge (28,297 km). The same managers estimated that there are over 3,500 km of streams where beaver could improve habitat conditions. The riparian width in streams with beaver ponds averaged 33.9 m (95 percent CI = 25.1-42.7 m) in contrast to 10.5 m (CI = 8.6-12.4 m) in streams without beaver. During waterfowl surveys we counted 7.5 ducks/km (CI = 0.9-14.4 ducks/km) of stream in areas with beaver ponds and only 0.1 ducks/km (no CIs calculated) of stream in similar areas without beaver present. Beginning in 1994, we restored beaver to 14 streams throughout Wyoming in an effort to create wetlands and improve riparian habitat. Waterfowl have been quick to respond to these important habitats. We feel that beaver restoration and management can be used to improve habitat in drainages where conflicts with other land uses are minimal.

(KEY TERMS: beaver; *Castor canadensis*; keystone; riparian; waterfowl; wetlands; Wyoming.)

INTRODUCTION

Through their dam-building activities, beaver alter stream systems by modifying channel geomorphology and hydrology. Beaver dams increase retention of sediment and organic matter, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity (Naiman *et al.*, 1988). The resulting habitats are rich mosaics of diversity that are beneficial hydrologically, biologically, and socially (Smith, 1980; Naiman *et al.*, 1988). While beaver often cause problems where they are in conflict with human activities (McKinstry and Anderson, 1999), they can be beneficial where they are used to maintain or improve riparian habitat.

Prior to the arrival of Europeans, the beaver population in North America was estimated to be between 60 and 400 million individuals (Seton, 1953; Naiman *et al.*, 1988). As eastern beaver populations declined from overharvest, expeditions were often made to the west (1800-1850), solely for the purpose of discovering new trapping areas (Cline, 1974; Kay, 1994). Eventually western regions were also overharvested (Johnson and Chance, 1974), and by 1900 beaver were nearly extirpated from North America (Jenkins and Busher, 1979). As an example of the level of beaver exploitation in the western U.S. during the height of trapping, Ogden (1950) recounts trapping 627 and 519 beaver in 200 and 150 km stretches, respectively,

¹Paper No. 01009 of the *Journal of the American Water Resources Association*. Discussions are open until August 1, 2002.

²Respectively, Research Scientist, Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, Laramie, Wyoming 82071; GIS Research Assistant, Spatial Data and Visualization Center, Box 4008, Laramie, Wyoming 82071-4008; and Unit Leader, Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, Laramie, Wyoming 82071 (E-Mail/McKinstry: markmck@uwyo.edu).

of the Humboldt River near present day Winnemucca, Nevada, in 1828 and 1829. Likewise, beaver were once reported to be "quite common" in the streams of Yellowstone National Park, but are now "ecologically absent" from this vast area for various reasons including overtrapping and overgrazing of native ungulates (Jonas, 1955; Russell, 1965; Kay, 1994). The elimination of beaver from portions of its historic range has been cited as a major influence on the change in structure and patterns of vegetation in these systems (Barnes and Dibble, 1986; Naiman *et al.*, 1986, 1988; Kay, 1994; Pollock *et al.*, 1995).

Riparian and wetland habitats in the mountainous west are thought to be valuable for waterfowl (Brown *et al.*, 1996) and other birds (Medin and Clary, 1990), yet no studies have been done to document their numerical influence. Wetland habitats in the ten western states have declined by approximately 53 percent since European settlement (Dahl, 1990) and reductions in beaver populations (Johnson and Chance, 1974) have added to this decline. Beaver wetlands are important to waterfowl in other portions of North America (Renouf, 1972; McCall *et al.*, 1996; Gabor *et al.*, 1999), but these areas are generally large, low gradient stream systems that flood broad areas. In contrast, beaver ponds in the western U.S. are usually located on streams with steeper gradients and incised channels that inundate relatively smaller areas. However, since these wetlands occur in arid regions where wetland habitats comprise less than 2 percent of the land area (Hansen *et al.*, 1995), they may be of even more importance to wetland dependent species. Furthermore, beaver wetlands in the mountain states are located within linear habitats (i.e., streams) that provide migration corridors and critical habitat to wildlife throughout various life stages.

Throughout the intermountain west, great interest has been expressed in improving riparian areas for wildlife, livestock, and humans (as reviewed by Johnson *et al.*, 1985; Clary *et al.*, 1992; Tellman *et al.*, 1993), and beaver are thought to be one tool that can be used to accomplish these goals (Apple, 1985; Albert and Trimble, 2000). In 1994 McKinstry and Anderson (1999) conducted a mail survey in response to increasing interest in beaver management and beaver reintroductions. The goals of this survey were to: (1) determine the attitudes of private and public-land managers towards beaver and beaver management in Wyoming, (2) determine current and future trends in beaver populations within the state, (3) assess the level of support for a beaver reintroduction program, and (4) identify areas that could benefit by the use of beaver for riparian enhancement. Partial results of the survey and population trends are reported in McKinstry and Anderson (1999). As a result of this

survey we initiated a beaver relocation program in 1994 to establish beaver in 14 streams where beaver had been extirpated (McKinstry and Anderson 1997; 2001; 2002). During these relocations, we also assessed waterfowl response to beaver ponds in various habitats.

Our first objective for the research reported here was to identify streams in Wyoming where beaver are currently present, extirpated, and where they are being used to manage riparian habitat. Our second objective was to identify streams where beaver could be used to create wetlands and improve riparian habitat. Our final objectives were to assess waterfowl use of habitat with and without beaver ponds, and to quantify the differences in the amount of wetland habitat between these two habitat types.

STUDY AREA AND METHODS

Beaver Occupancy

We surveyed 125 public-land managers/wildlife biologists from the U.S. Forest Service, Bureau of Land Management (BLM), Wyoming Association of Conservation Districts, and Wyoming Game and Fish Department (WG&FD) for their knowledge on beaver occupancy for streams within their district. Each manager was sent 1:100,000-scale BLM topographic maps covering their district and instructions to highlight stream reaches according to four categories: (1) currently occupied by beaver, (2) beaver were once present but are now extirpated, (3) riparian management is being actively pursued using beaver management, and (4) beaver could be used to improve riparian habitat. The managers were asked to limit their reporting to stream reaches for which they had direct and reliable knowledge, and not to speculate on beaver occupancy for other streams. A total of 56 1:100,000-scale maps cover Wyoming; we received information on beaver occupancy for 48 of those maps, or approximately 88 percent of the total stream length in Wyoming (175,803 km). The eight maps for which we did not receive information included the two that covered Yellowstone National Park (no information was requested from Yellowstone Park) and six others where managers simply did not supply information.

The information from each map was transferred to a Geographic Information System (GIS) using ARC INFO and ARCVIEW (ESRI, 1998) and the digital line graph 1:100,000-scale coverage for Wyoming (Wyoming Gap Analysis, 1996). Each arc (stream segment) within the coverage was assigned one of the

four identifications for beaver occupancy listed above, or was left blank to code for no information. Where a manager's highlighting did not extend entirely to the end of a stream reach where a node was located (nodes allowed us to assign attributes defined as 1 through 4 above – to stream reaches between nodes), we extended the classification to the next node (1 percent of stream highlights). The procedure Calculate in Arcview (ESRI, 1998) was used to generate total stream lengths by stream order and the four categories of beaver occupancy.

Waterfowl Use and Wetland Area

To compare waterfowl use in areas with and without beaver we selected eight paired (16 total) 1-km reaches located throughout Wyoming on first- through third-order streams. Each paired site was located within similar habitat types and with no human-caused disturbance (e.g. roads, grazing, timber management, development, etc.), so the only difference between sites was the presence or absence of beaver and, consequently, wetland habitat. At six paired locations the paired reaches were located on the same stream, either up or downstream of each other. For the remaining two locations, we selected adjacent streams just across the stream divide. In order to accurately represent habitat types in which beaver are found, we selected two paired sites within both cottonwood and aspen (*Populus* spp.) dominated habitats and four paired sites within willow (*Salix* spp.) communities. The start of each survey point was selected randomly within each stream reach. Waterfowl were surveyed by walking the 1-km stream reaches and recording all waterfowl observed within the riparian zone. Species and gender were recorded for each bird observed. All surveys were conducted in 1996 from May 15 through June 15 and between 0700 and 1000 hours in an attempt to survey active breeding birds.

In addition to the paired stream surveys, we assessed waterfowl use at 31 beaver ponds created by beaver that we relocated to 13 sites throughout Wyoming. These relocations, and their success, are described in more detail in McKinstry and Anderson (1997; 2001; 2002). At each of the relocation sites we walked the shorelines of the ponds and recorded all wildlife seen during two visits from June 1 to July 15, between the hours of 0700 and 1000. These sites were sampled the year following creation of the initial dam.

To quantify the amount of wetland habitat created by beaver we measured wetland width (total width of area considered wetland using the definition from Cowardin *et al.*, 1979) at 100-m intervals along the same paired stream reaches that we used to assess

waterfowl numbers. All measurements were taken perpendicular to the shoreline and averaged for each stream segment. We then averaged these composite measurements and computed 95 percent CIs. We present CIs in order for the reader to make a comparison between our estimates and judge for themselves the significance of our results (Johnson, 1999).

RESULTS

We received surveys from 72 resource managers (58 percent), providing information on beaver occupancy for 18 percent of the streams covered by the 48 maps (Table 1). Beaver currently occupy 58 percent of streams reported by managers and are missing from 24 percent of streams where it is thought they were once abundant. Beaver removal has occurred primarily on first- to fifth-order streams (Figure 1). Managers also reported that they knew of over 3,500 km of streams where beaver could be used for habitat improvement (Table 1). The majority of these areas were in first- to third-order stream systems where beaver can have the biggest impact.

A total of 61 waterfowl, representing seven different species, were counted during our paired stream surveys. Species seen included green-winged teal (*Anas crecca*) (19), mallards (*A. platyrhynchos*) (18), blue-winged teal (*A. discors*) (12), cinnamon teal (*A. cyanoptera*) (5), wood ducks (*Aix sponsa*) (3), gadwalls (*A. strepera*) (2), and American wigeon (*A. americana*) (1). Beaver-ponded stream reaches (eight total) averaged 7.5 ducks/km (95 percent CI = 0.6-14.4) of stream. Additionally, four broods (two green-winged teal, one mallard, and one blue-winged teal) were counted during the surveys of beaver-pond reaches, supporting our belief that beaver ponds are important for breeding waterfowl and their broods. A single blue-winged teal was the only duck seen on the 8 km of stream reaches without beaver. While surveying 31 newly created ponds (less than two years old) at our relocation sites, we found three mallard hens and one blue-winged teal hen, of which all but one mallard hen were tending active nests.

The wetland width in streams with beaver ponds averaged 33.9 m (95 percent CI = 25.1-42.7 m) and 10.5 m (95 percent CI = 8.6-12.4 m) in streams without beaver. Converting to hectares we see almost a three-fold increase in wetland habitat in areas with beaver [3.4 ha (95 percent CI = 2.7-4.1 ha) vs. 1.1 ha (95 percent CI = 0.8-1.3 ha)].

We relocated beaver to 14 different streams where they had been extirpated and they eventually created 31 ponds within one year of their release (other ponds have been created since). Eight of these ponds filled

TABLE 1. Total Stream Lengths, by Stream Order, for 48/56 1:100,000 Scale Maps in Wyoming Along With Beaver Presence and Absence, and Stream Lengths Where Beaver Are Being Used or Could be Used for Riparian Enhancement. Information was reported from 72 resource managers and incorporated into a GIS for calculation purposes.

Stream Order	Total Stream Length (km)	Total km Reported (percent of total stream length)	Beaver Currently Present (km) (percent of reported)	Beaver Currently Absent (km) (percent of reported)	Beaver Currently Used for Riparian Management (km)	Possible Introduction Areas (km)
1	95,138	11,663 (12%)	6,880 (59%)	2,865 (25%)	282	1,487
2	26,859	5,583 (21%)	3,007 (54%)	1,449 (26%)	133	780
3	14,962	4,231 (28%)	2,331 (55%)	947 (22%)	81	552
4	8,169	2,869 (35%)	1,588 (55%)	634 (22%)	49	346
5	4,288	1,619 (38%)	899 (56%)	371 (23%)	6	215
6	2,035	1,120 (55%)	775 (69%)	118 (11%)	44	228
7	2,597	1,211 (47%)	1,070 (88%)	113 (9%)	14	20
Total	154,048	28,297 (18%)	16,550 (58%)	6,497 (23%)	609	3,628

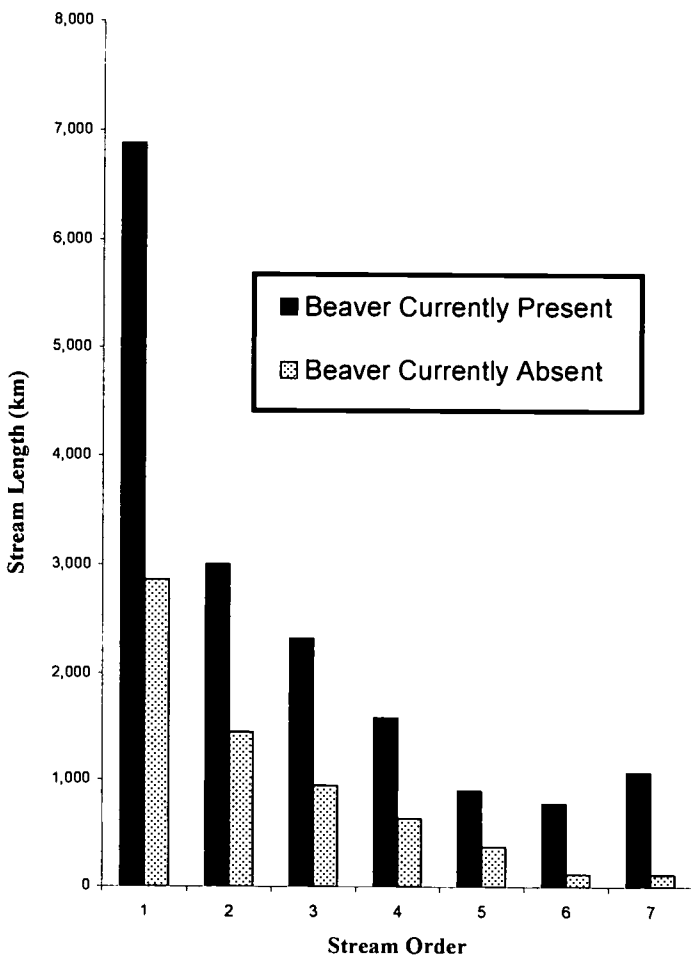


Figure 1. Beaver Presence and Absence (km of stream), by Stream Order, for 23,047 km of Streams in Wyoming as Reported by 72 Resource Managers.

with sediment within one year of their construction and the beaver eventually created new ponds in the drainage. At four of the sites where beaver have been established for over three years, several pond complexes have been constructed and the offspring are now constructing ponds elsewhere in the drainage.

DISCUSSION

Paine (1969) defined “keystone species” as those that help communities to persist in time through “their activities and abundances.” Power *et al.* (1996) further refined the idea of a keystone species as one whose effect is “disproportionately larger” than would be predicted from their abundance and suggested that the term has been overused. Beaver are perhaps the best and possibly only example of a “habitat-modifying keystone species” (Power *et al.*, 1996), and they broadly impact many different species as well as ecosystem processes (as reviewed in Naiman *et al.*, 1988). As an example of the amount of habitat that beaver provide, Munther (1982, 1983) reported that the average creek in the northern Rockies without beaver provides between 0.8 and 1.6 ha/km of wetland habitat, whereas the same creek with beaver activity can provide over 9.6 ha/km of wetland habitat. Our estimates of wetland habitat in areas dominated by beaver ponds were lower than estimates from Munther (1982, 1983), but still substantially greater than those areas without beaver.

Other researchers (Renouf, 1972; Peterson and Low, 1977; Smith, 1992; Grover and Baldassarre,

1995) have examined the importance of beaver habitats to waterfowl; however, most have focused on specific habitat variables associated with beaver ponds and not the overall impact (e.g., numerical) beaver have on waterfowl populations across a broad region. While Gabor *et al.* (1999) also focused on beaver pond management and demonstrated that different variables associated with beaver ponds can impact waterfowl, they also commented that breeding waterfowl densities on beaver ponds in southern Ontario are some of the highest within the province. In Maine, where beaver have an enormous impact on the amount of wetland habitat, the number of beaver and level of trapping pressure were shown to have a positive and negative impact, respectively, on waterfowl populations (McCall *et al.*, 1996). In the western U.S., beaver ponds provide isolated breeding-pair ponds for waterfowl at a time in their annual life-cycle when isolation of each breeding pair is critical to courtship and overall breeding success (as reviewed in Batt *et al.*, 1992). Within these ponds, hens find the necessary protein and calcium-rich foods (i.e., invertebrates) that maintain their condition during egg laying. Additionally, beaver ponds serve as brood-rearing ponds in late summer when duckling broods need the same high-protein foods necessary for growth and development prior to fledging (as reviewed in Batt *et al.*, 1992). Wyoming is currently ranked fifth or sixth of the 50 states in waterfowl production (Kelly *et al.*, 1995), and beaver undoubtedly play a role in this production.

Our research suggests that beaver may have a large impact on waterfowl populations within Wyoming. While we do not have direct evidence of beaver's impact to waterfowl populations on a landscape scale, if we extrapolate our results to only the first- to third-order streams for which managers thought that beaver could be used to improve habitat, we estimate that the removal of beaver from these streams [2819 km total (Table 1, column 7, rows 1 through 3)] may have reduced habitat for up to 19,000 ducks. If we continue, and assume that the percent of streams where beaver have been removed (24 percent) is representative of the state, and only extrapolate to first- to third-order streams [32,870 km (Table 1, column 2, rows 1 through 3)], the reduction in beaver habitat could impact over 240,000 waterfowl statewide. We feel that the removal of beaver has also caused a significant reduction in wetland habitat (up to 275,000 ha statewide). This habitat loss may be especially detrimental when you consider that these wetlands are not ephemeral and can provide habitat during dry seasons (August through October) and dry years (Brown *et al.*, 1996). Since the managers we surveyed only reported on 18 percent of the total stream length within the state, we caution that our

results may not be representative of the entire state. However, we feel that these figures may actually underestimate the number of streams where beaver have been removed since these managers were primarily reporting about streams on public land, and they may have underreported streams on private land where beaver extirpation is probably more widespread (McKinstry and Anderson, 1999).

We realize that experimental studies have not been done directly linking waterfowl population levels and wetland habitat with beaver abundances. However, our results suggest that beaver are fulfilling an important role in supporting Wyoming's waterfowl and other wetland-dependent species. Furthermore, we argue that reductions in historic beaver populations have altered the structure and function of Wyoming's riparian areas, and consequently the populations of wildlife that depend upon these systems. Many drainage areas within the state (e.g., Sweetwater River, Green River, Powder River, and Big Horn River) historically had large numbers of beaver associated with them (M. McKinstry, personal observation of historical dams) and currently only scattered populations exist. Overtrapping in the early to mid 1800s, conflicts with human activities (e.g. irrigation, road building), and general intolerance have reduced beaver populations dramatically (Johnson and Chance, 1974; Jenkins and Busher, 1979). These declines have almost certainly impacted populations of wetland-dependent species, although no studies have addressed this issue. We suggest that further work needs to be done regarding the impact that beaver have on structuring habitat and wildlife populations in the western U.S.

We were successful at reintroducing beaver (defined as a breeding pair establishing a dam and lodge within 2 km of the release site) at 13 of our 14 sites in Wyoming (McKinstry and Anderson, 2001; 2002). Predation and emigration losses accounted for 60 percent of our released beaver (McKinstry and Anderson, 2001; 2002), and on average it took 17 beaver to successfully colonize a stream (McKinstry and Anderson, 2001; 2002). Although our introductions were more labor intensive than we had originally planned (e.g., high predation and emigration necessitated more releases), we were able to establish beaver in a broad range of habitats throughout the state. At all sites, we observed wildlife directly using the ponds the first year they were created. Waterfowl response to these new wetlands was particularly impressive when you consider that several birds were reproducing at the sites. Our program was considered a success and enjoyed support from a broad range of people and interest groups including private landowners, state and federal agencies, NGOs, citizen's groups, academia, and sportspeople. The relocation

program is now continuing under the direction of the WG&FD, which is using contract trappers to conduct the trapping and relocations.

Simberloff (1998) argues that keystone species "unite the best features of single-species and ecosystem management" strategies and that managing keystones can be an efficient method to manage ecosystems. This view is not shared by all (Mills *et al.*, 1993; Power *et al.*, 1996), but in the case of beaver it is difficult to argue that their influence is not critical in a state where less than 2 percent of the habitat is considered wetland, and yet over 80 percent of wildlife species are dependent upon this habitat during some life stage (Hansen *et al.*, 1995).

ACKNOWLEDGMENTS

We thank the Wyoming Game and Fish Department, U.S. Fish and Wildlife Service, Jack's Plastic Welding, Ducks Unlimited, National Rifle Association, Rocky Mountain Elk Foundation, National Fish and Wildlife Foundation, North American Wetlands Conservation Council, University of Wyoming, and the George E. Menkens Memorial Scholarship for funding this research; and T. Bragg, the Breteche Creek Foundation, A. Larrick, T. Malmberg, M. Miller, the Bureau of Land Management, the State of Wyoming, and numerous landowners for allowing us access to study sites. R. Karhu, S. Rothmeyer, S. Mohren, K. Rompola, and E. Hardgrave provided excellent field assistance. Critical reviews of the manuscript by N. Nibbelink, J. Roaldson, K. Gordon, and three anonymous reviewers were much appreciated and improved the manuscript dramatically.

LITERATURE CITED

- Albert, S. and T. Trimble, 2000. Beavers Are Partners in Riparian Restoration on the Zuni Indian Reservation. *Ecological Restoration* 18:87-92.
- Apple, L. L., 1985. Riparian Habitat Restoration and Beavers. *In: Riparian Ecosystems and Their Management: Reconciling Conflicting Uses*, R. R. Johnson, C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre (Editors). USDA Forest Service, General Technical Report RM-120, Rocky Mountain Research Station, Fort Collins, Colorado, pp. 489-490.
- Barnes, W. J. and E. Dibble, 1986. The Effects of Beaver in Riverbank Forest Succession. *Canadian Journal of Botany* 66:40-44.
- Batt, B. D., A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu (Editors), 1992. *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis, Minnesota, 635 pp.
- Brown, D. J., W. A. Hubert, and S. H. Anderson, 1996. Beaver Ponds Create Habitat for Birds in Mountains of Southeastern Wyoming. *Wetlands* 16:127-133.
- Clary, W. P., E. D. McArthur, D. Bedunah, and C. L. Wambolt (Compilers), 1992. *Proceedings, Symposium on Ecology and Management of Riparian Shrub Communities*. USDA Forest Service General Technical Report INT-289, Intermountain Research Station, Ogden, Utah, 232 pp.
- Cline, G. C., 1974. *Peter Skene Ogden and the Hudson's Bay Company*. University of Oklahoma Press, Norman, Oklahoma, 279 pp.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe, 1979. *Classification of Wetlands and Deep Water Habitats of the United States*. U.S. Fish and Wildlife Service, Biological Report 79/31, Washington, D.C., 131 pp.
- Dahl, T. E., 1990. *Wetlands Losses in the United States 1780's to 1980's*. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C., 13 pp.
- ESRI (Environmental Systems Research Institute), 1998. *ArcView Version 3.1*. Redlands, California.
- Gabor, T. S., H. R. Murkin, J. W. Ingram, R. T. Clay, and R. F. Maher, 1999. *Beaver Pond Management Assessment Program (1993-1997)*. Unpublished Final Report, Institute for Wetland and Waterfowl Research, c/o Ducks Unlimited Canada, Stonewall, Manitoba, Canada, 77 pp.
- Grover, A. M. and G. A. Baldassarre, 1995. Bird Species Richness Within Beaver Ponds in South-central New York. *Wetlands* 15:108-118.
- Hansen, P. L., R. D. Pfister, K. Boggs, B. J. Cook, J. Joy, and D. K. Hinckley, 1995. *Classification and Management of Montana's Riparian and Wetland Sites*. Miscellaneous Publication No. 54, Montana Forest and Conservation Experiment Station, School of Forestry, The University of Montana, Missoula, Montana, 646 pp.
- Jenkins, S. H. and P. E. Busher, 1979. *Castor Canadensis: Mammalian Species No. 120*. American Society of Mammalogists, Shippensburg, Pennsylvania, 8 pp.
- Johnson, D. H., 1999. The Insignificance of Statistical Significance Testing. *Journal of Wildlife Management* 63:763-772.
- Johnson, D. R. and D. H. Chance, 1974. Presettlement Overharvest of Upper Columbia River Beaver Populations. *Canadian Journal of Zoology* 52:1519-1521.
- Johnson, R. R., C. D. Ziebell, D. R. Patton, P. F. Ffolliott, and R. H. Hamre (Technical Coordinators), 1985. *Riparian Ecosystems and Their Management: Reconciling Conflicting Uses*. USDA Forest Service General Technical Report RM-120, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, 523 pp.
- Jonas, R. J., 1955. *A Population and Ecological Study of the Beaver (Castor canadensis) of Yellowstone National Park*. M.S. Thesis, University of Idaho, Moscow, Idaho, 193 pp.
- 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.
- Kelly, S. T., R. J. Blohm, J. P. Bladen, and H. C. Bourne, 1995. Trends in Duck Breeding Populations, 1995-1989. U.S. Department of Interior. FWS/MBMO Administrative Report.
- McCall, T. C., T. P. Hodgman, D. R. Diefenbach, and R. B. Owen, Jr., 1996. Beaver Populations and Their Relation to Wetland Habitat and Breeding Waterfowl in Maine. *Wetlands* 16:163-172.
- McKinstry, M. C. and S. H. Anderson, 1997. Use of Beaver to Improve Riparian Areas in Wyoming. *In: Wyoming Water 1997: Applied Research for Management of Wyoming's Water Resources*, C. Goertler, C. Rumsey, T. Bray and D. Boysen (Editors). Wyoming Water Research Center, Laramie, Wyoming, pp. 128-134.
- 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, 2001. Mortality and Emigration of Transplanted Beaver in Wyoming. *In: Proceedings North American Aquatic Furbearer Symposium*, Mississippi State University, Mississippi State, Mississippi (in press).
- McKinstry, M. C. and S. H. Anderson, 2002. Fates of Transplanted Beaver in Wyoming. *Canadian Field-Naturalist* (in press).

- Medin, D. E. and W. P. Clary, 1990. Bird Populations in and Adjacent to a Beaver Pond Ecosystem in Idaho. USDA Research Paper INT-432, Intermountain Research Station, Ogden, Utah, 6 pp.
- Mills, L. S., M. E. Soule, and D. F. Doak, 1993. The Keystone-Species Concept in Ecology and Conservation. *Bioscience* 43:219-223.
- Munther, G. L., 1982. Beaver Management in Grazed Riparian Ecosystems. *In: Wildlife Livestock Relationships Symposium: Proceedings 10*, J. M. Peek and P. D. Dalke (Editors). University of Idaho, Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho, pp. 234-241.
- Munther, G. L., 1983. Integration of Beaver Into Forest Management. Paper Presented at Colorado/Wyoming Chapter of American Fisheries Society, Laramie, Wyoming.
- Naiman, R. J., C. A. Johnston, and J. C. Kelly, 1988. Alteration of North American Streams by Beaver. *Bioscience* 3:753-762.
- Naiman, R. J., J. M. Melillo, and J. E. Hobbie, 1986. Ecosystem Alteration of Boreal Forest Streams by Beaver (*Castor canadensis*). *Ecology* 67:1254-1269.
- Ogden, P. S., 1950. Peter Skene Ogden's Snake Country Journal, 1826-27. *In: Hudson's Bay Record Society Publication 23*, K. G. Davies and A. M. Johnson (Editors). London, United Kingdom, 283 pp.
- Paine, R. T., 1969. A Note on Trophic Complexity and Community Stability. *American Naturalist* 103:91-93.
- Peterson, S. R. and J. B. Low, 1977. Waterfowl Use of Uinta Mountain Wetlands in Utah. *Journal of Wildlife Management* 41:112-117.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay, 1995. Beaver as Engineers: Influences on Biotic and Abiotic Characteristics of Drainage Basins. *In: Linking Species and Ecosystems*, C. G. Jones and J. H. Lawton (Editors). Chapman and Hall, New York, New York, pp. 117-126.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Casilla, J. Lubchenco, and R. T. Paine, 1996. Challenges in the Quest for Keystones. *Bioscience* 46:609-620.
- Renouf, R. N., 1972. Waterfowl Utilization of Beaver Ponds in New Brunswick. *Journal of Wildlife Management* 36:740-744.
- Russell, O., 1965. *Journal of a Trapper*. University of Nebraska Press, Lincoln, Nebraska, 191 pp.
- Seton, E. T., 1953. *Lives of Game Animals. Part 2, Rodents, etc.* Doubleday, Doran, Garden City, New York, Vol. 4, pp. 443-949.
- Simberloff, D., 1998. Flagships, Umbrellas, and Keystones: Is Single-Species Management Passé in the Landscape Era? *Biological Conservation* 83:247-257.
- Smith, B. H., 1980. Not All Beaver Are Bad; Or, An Ecosystem Approach to Stream Habitat Management, With Possible Software Applications. *In: Proceedings 15th Annual Meeting, Colorado-Wyoming Chapter American Fisheries Society*, Feb. 27-28, Fort Collins, Colorado, pp. 32-36.
- Smith, D. F., 1992. Avian Use of Beaver-Created Wetlands in Northern Wisconsin. M.S. Thesis, University of Wisconsin, Stevens Point, Wisconsin, 38 pp.
- Tellman, B., H. J. Cortner, and M. G. Wallace (Technical Coordinators), 1993. *Riparian Management: Common Threads and Shared Interests*. USDA Forest Service General Technical Report RM-226, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 419 pp.
- Wyoming Gap Analysis, 1996. 1:100,000-Scale Hydrography for Wyoming (enhanced digital line graph). Spatial Data and Visualization Center, Laramie, Wyoming.