Composition of Beaver Colonies in Damage Sites of the Southeastern United States

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Abstract: Natural resource managers faced with resolving beaver damage may make decisions based on classic literature suggesting that beavers (*Castor canadensis*) are monogamous breeders that live in colonies composed of a breeding pair of adults, their offspring, and occasionally the offspring from the previous year; and that beavers typically breed during the winter months and bear their offspring in the spring. We analyzed colony composition at 89 damage sites in seven southeastern states and found deviations from these classic studies. Colony size ranged from 2 to 18 individuals ($\chi = 5.66$, SE = 0.36). Eleven colonies contained one male and one female only, yet only five of those were breeding pairs. Colonies contained from 1 to 11 males, whereas the number of females among colonies ranged from 0 to 8. Mean age of beaver within a colony across all states was 3 years (SE = 0.2); age ranged from 1 to 20 years; but 30% of all individuals comprised the 1-year age class. Breeding females were found in every age class except the 0- and 1-year age classes. At least one breeding female was found in 78% of all colonies and >1 breeding female was present in 17% of all colonies sampled. The youngest reproductively-active female was 2 years old; the oldest was 18 years old. Lactating and/or pregnant females were captured in every month except September, October, and November, which suggests beavers exhibit a flexible or extended breeding season in the Southeast. Knowledge of the potential composition of beaver colonies may be important when making management decisions to reduce damage.

Key words: beaver, *Castor canadensis*, colony composition, management

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The North American beaver (*Castor canadensis*) has shaped North America's landscape for hundreds of years and commonly is referred to as a keystone species and an ecosystem engineer. Their damming behavior creates valuable wetland habitat for fishes, waterfowl, song birds, reptiles and amphibians, and hundreds of wetland plants. Conversely, the damming of water in certain places (e.g., road culverts) negatively affects private and public lands. The negative impacts of beavers on timber, agriculture, and transportation networks alone cause millions of dollars of economic losses every year in southeastern states (Arner and DuBose 1982). The National Wildlife Research Center (NWRC) reports that the U.S. Department of Agriculture's Wildlife Services (WS) program in Mississippi saved between $1 million and $40 million annually by managing beaver damage (Shwiff and Kirkpatrick 2008).

Several different management tools and techniques are available to manage beaver populations and the damage they cause. Current beaver management strategies fall into three distinct categories: removal of the beavers, protection of the resource sustaining damage, or a combination of the two. The method of management selected depends on the resource being protected, which in turn often determines the most appropriate strategy. Removing individual beavers through trapping allows the manager to protect a resource by removing the individual responsible for the damage but may require more commitment than some non-lethal measures. A physical barrier, such as deep water fencing, is a resource protection and management tool designed to prevent damming activities. Deep water fences commonly are used at road culverts to exclude beaver from accessing the culvert. Physical barriers are also constructed around food sources to protect them from girdling. Water control structures are used to manage water levels in areas that beavers have dammed. Lethal and non-lethal management tools are often used in conjunction to manage a beaver colony damaging a resource.

If beaver management is to be successful, managers must understand the underlying dynamics of beaver colonies occurring in their area. Failure to remove problem animals may lead to more complex problems, as these individuals can cause damage to unprotected resources up or downstream from the home colony. Additionally, beavers left alone may continue to reproduce and will add individuals to the population, potentially exacerbating damage problems locally. In areas where beaver populations are large, juveniles often disperse into sub-optimal habitat (DeStefano et al. 2006) or may remain in their natal colony for longer periods of time (McNew and Woolf 2005). In either situation, damage is likely to increase in areas that previously were unaffected.

When developing beaver management strategies, managers should consider both the social parameters and reproductive dynamics of beaver colonies as well as overall population size. Aerial surveys of lodges and dams, spotlight counts, and mark recapture methods all assume certain excepted social parameters of beaver colony composition when predicting population sizes (Swafford 2003). If these assumptions about social parameters are false, serious errors in estimating beaver population size may occur. Recent genetic research conducted in central and southern Illinois has shown that beaver pairs are not strictly monogamous as previously thought. Crawford et al. (2009) found that many females located in southern Illinois were first order relatives, suggesting female philopatry. Likewise, they found evidence of gene flow among colonies, indicating that inter-colony mating occurred.

This study was conducted to examine the social structure of beaver colonies occurring in the southeastern United States. Since the most current research conducted on beaver colony composition, movements, and genetic make-up have all occurred in more northern latitudes, we believe it is important to examine beaver colony composition in the southeastern United States to allow managers to make more informed decisions when implementing beaver management. Our objective was to investigate the social structure of beaver colonies in the southeastern United States and determine possible management implications for sites that experience repeated damage.

Methods

Beavers were obtained from areas where beaver damage occurred in seven states in the southeastern United States (Alabama, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia) and were under a cooperative agreement between landowners and WS. The collection method for the study was trapping only, and WS personnel participating in the study reported no signs of recreational or private trapping activity during the duration of sampling. We assumed these sites sustained high beaver populations and that habitat was not a limiting factor. Beavers were trapped for a period of 18 months from December 2003 to May 2005 and encompassed two complete trapping years (year 1 = December 2003–November 2004, year 2 = December 2004–November 2005) with an additional six months of data. All trapping was conducted by specialists of the USDA Animal and Plant Health Inspection Service (APHIS) WS programs while conducting normal damage management activities. WS specialists focused on damage locations with evidence of beaver activity and continued trapping until all the individuals in the colony were collected. Special attention was given to remove entire colonies as quickly as possible not only to reduce damage impacts, but to minimize chances for immigration.

Jaw bones were extracted from all beavers. Age was estimated by replacement of the temporary premolar and basal closure of the mandibular molars as described by Van Nostrand and Stephenson (1964), Larson and van Nostrand (1968), and Woodward (1977). Beavers were aged and placed into 1 of 10 age categories and segregated in half year increments, beginning at 0.0 – 0.5 years and ending with 4.5 – ≥5.0 years. The M1 teeth of all samples aged to ≥3 years were sent to Matson's Laboratory (Milltown, Montana) for cementum age analysis. In addition, 25 M1 teeth were selected randomly from the remaining age groups and shipped to Matson's Laboratory for analysis ($n = 370$ teeth sent for cementum annuli aging). Age groups later were converted to five age classes for comparison analysis: 0 = 0.0 to <1.0, 1 = ≥1.0 to <2.0, 2 = ≥2.0 to <3.0, 3 = ≥3.0 to <4.0, 4 = ≥4.0 to <5.0, and 5 = ≥5.0.

Sex was determined by necropsy. Females were designated as reproductive females when there was evidence of fetuses, lactation, placental scars, corpora lutea, and/or corpus albacantia. Female reproductive tracts were removed in the field, immediately frozen, and later necropsied to collect productivity data. Ovaries were removed from the reproductive tract, cleaned, and weighed to the nearest hundredth of a gram. Ovary lengths and widths were taken with digital calipers and recorded to the nearest tenth of a millimeter. A cross-section was taken from each ovary to determine the number of corpora lutea, corpora albicantia, placental scars, and the placental length. Placental horn length was documented by placing the horn ventral side up and measuring it from the junction of the horn to the tip of the ovary. If fetuses were present at the time of necropsy, weight (g) and length (mm) were recorded.

Results

We collected 504 beavers from 89 distinct colonies across seven southeastern states over a trapping period of 18 months (Figure 1).

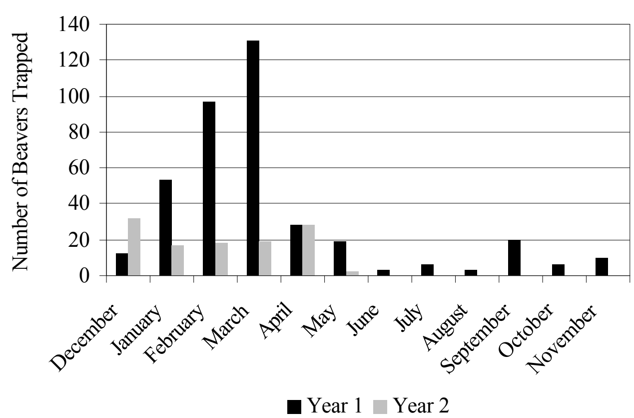

Figure 1. Number of beaver collected by month at 89 damage sites throughout seven states in the southeastern United States, December 2003–November 2004 (Year 1) and November 2004–December 2005 (Year 2).

Table 1. Mean beaver colony size and composition by sex and age class (0-≥5) at 89 damage sites in the southeastern United States, December 2003–May 2005.

State	Number of colonies	Mean (SE) days of trapping effort	Mean (SE) colony size	Mean (SE) number of males/colony	Mean (SE) male age class	Mean (SE) number of females/colony	Mean (SE) female age class
AL	4	20.3 (8.97)	7.75 (1.79)	4.0 (1.47)	2.00 (0.4)	3.75 (0.85)	2.00 (0.49)
GA	13	5.07 (1.16)	6.69 (1.21)	3.54 (0.76)	2.00 (0.3)	3.15 (0.54)	2.00 (0.27)
MS	40	15.1 (2.51)	4.82 (0.44)	2.40 (0.25)	2.00 (0.2)	2.42 (0.28)	2.00 (0.19)
NC	15	10.1 (2.14)	5.53 (0.85)	3.13 (0.64)	2.00 (0.3)	2.40 (0.46)	3.00 (0.32)
SC	11	16.7 (5.12)	7.18 (1.24)	4.00 (0.82)	2.00 (0.3)	3.18 (0.52)	2.00 (0.33)
TN	2	31.8 (22.5)	8.00 (3.0)	4.50 (0.50)	4.00 (0.8)	3.50 (2.50)	4.00 (0.53)
VA	4	5.00 (3.36)	3.75 (0.85)	1.75 (0.25)	3.00 (0.8)	2.0 (0.82)	2.00 (0.63)
Totals	89	13.16 (1.54)	5.66 (0.36)	3.30 (0.4)	2.00 (0.3)	2.90 (0.30)	2.40 (0.30)

WS trappers invested 1,171 trapping days during the study and trapping effort was applied to sites when beaver damage occurred, regardless of season. Mean trapping effort to remove entire colonies was 13.6 days (SE 1.5; Table 1).

Colony Composition

Beaver colony size ranged from 2 to 18 beavers with a mean of 5.66 beavers per colony (SE = 0.36). Mean number of males per colony were 3.3 (SE=0.4) and mean number of females were 2.9 (SE = 0.3; Table 1). Male beavers were represented in every colony sampled. Three colonies were comprised only of male beavers, in which total group size was three in all cases. Eleven colonies contained one male and one female only, although only 5 of the 11 colonies were characterized as breeding pairs. Colony composition for males ranged from 1 to 11 individuals; females ranged from 0 to 8 individuals.

The largest number of beavers captures (*n* = 229) occurred during winter (December, January, and February), whereas the greatest number of captures per month occurred in March (*n*=150). Spring, fall, and summer captures were 227, 36, and 12 beavers, respectively, although the summer months were only sampled in 2004.

Sex Ratios

Of the 504 individual beavers captured, 53% (*n* = 265) were males and 47% (*n* = 239) were females. We observed slight differences in the sex ratio within certain age classes (Figure 2). We found the ≥5-year age class and the 2-year age class both were dominated by females; males were more prevalent in all other age classes. In the ≥5-year age class, 119 individuals were collected, of which 55 were males and 64 were females (1:1.16 sex ratio).

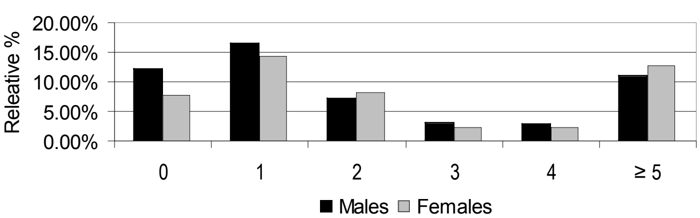

Figure 2. Relative percentages of trapped beaver among age classes by sex at 89 damage sites in the southeastern United States, December 2003–May 2005.

Age Structure

Of 504 beavers captured, 51% (*n* = 255) were juveniles (<2 years); 49% (*n* = 249) were adults (≥2 years). The mean number of juveniles per colony was 3 (SE = 0.2) and ranged from 0 to 10. The mean number of adults per colony also was 3 (SE = 0.2) and ranged from 0 to 12. The largest age class was the 1-year class (*n* = 155), which represented 30% of the total sample size. The smallest age class was the 4-year class (*n* = 26; 5% of the total sample). The mean age class of males for all states was 2.0 (SE = 0.3); females was 2.4 (SE = 0.3). True mean age, based on cementum annuli analyses, was 2.6 (SE = 0.1) for males and 3.4 (SE = 0.3) for females. Males were more prevalent in every age class except for the 2-year and ≥5-year age classes (Figure 2). The oldest male trapped was 20 years of age and the oldest female was 18.

Female Productivity

Although we found a mean of 1 breeding female per colony (SE = 0.08), only 78% (*n* = 69) of the 89 colonies sampled yielded ≥1 breeding female per colony (Table 2). Sixteen colonies (17%) contained >1 breeding female, 4 of which contained ≥3 breeding females (Table 2). The maximum number of breeding females found in an individual colony was four. Four colonies in Mississippi each contained two breeding females, both of which were lactating. The mean days between the capture of breeding females for the colonies was 12.5 (SE = 6.27), but two of the Mississippi colonies had only 2 days of trapping between pregnant female capture dates.

Ninety female beavers were breeding during the study (37% of all females trapped). Seventy-five females trapped were either pregnant with fetuses or lactating. Lactating and pregnant females were trapped in every month of the year except for September, October, and November (Figure 3). From December 2003 through

Table 2. Female composition of beaver colonies containing breeding females at 87 damage sites in the southeastern United States, December 2003–May 2005.

State	Number of colonies	Mean (SE) colony size	Mean (SE) number of females/colony	Mean (SE) number of non-breeding females/colony	Mean (SE) number of breeding females	Mean (SE) breeding female age
AL	4	7.75 (1.79)	3.75 (0.85)	3.25 (0.63)	0.05 (0.28)	5.00 (3.00)
GA	13	6.69 (1.21)	3.15 (0.54)	2.00 (0.42)	1.15 (0.22)	5.85 (0.86)
MS	40	4.82 (0.44)	2.42 (0.28)	1.42 (0.23)	1.00 (0.11)	6.71 (0.66)
NC	15	5.53 (0.85)	2.40 (0.46)	1.40 (0.33)	1.00 (0.17)	8.40 (1.30)
SC	11	7.18 (1.24)	3.18 (0.52)	2.00 (0.47)	1.18 (0.29)	5.28 (0.72)
TN	2	8.00 (3.0)	3.50 (2.50)	1.50 (1.50)	2.00 (1.00)	6.00 (1.95)
VA	4	3.75 (0.85)	2.00 (0.82)	1.25 (0.63)	0.75 (1.00)	7.00 (4.50)
Totals	89	5.66 (0.36)	2.90 (0.30)	1.66 (0.15)	1.01 (0.08)	6.63 (0.43)

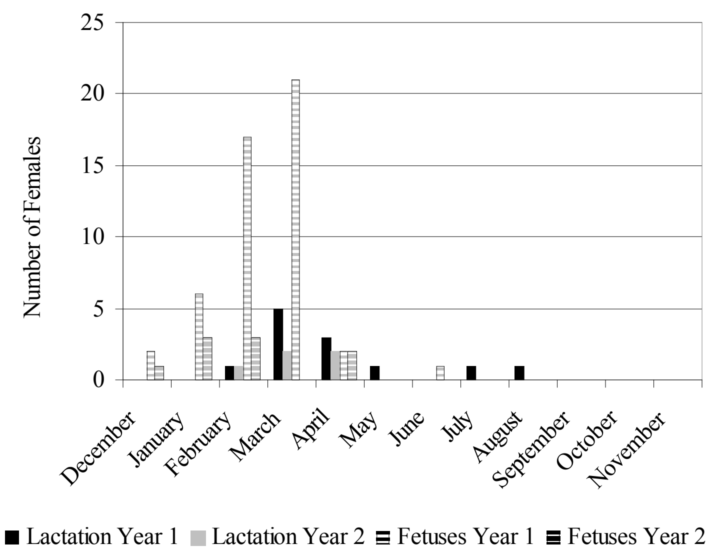

Figure 3. Number of lactating and pregnant female beavers trapped at 89 damage sites in the southeastern United States by month, December 2003–Novemver 2004 (Year 1) and November 2004–December 2005 (Year 2).

November 2004, the greatest number of lactating and pregnant females were captured from December through April; the maximum number by month peaked in March ($n = 26$), followed by February ($n = 18$) and January ($n = 6$). One pregnant or lactating female was trapped each month from May through August in 2004 ($n = 4$).

We also documented the presence of multiple pregnant females per colony. Multiple pregnant females occurred in 10% ($n = 9$) of the 89 colonies sampled. Colonies that yielded multiple pregnant females occurred in South Carolina ($n = 2$), Georgia ($n = 2$), Mississippi ($n = 3$), and North Carolina ($n = 2$). One colony in Georgia contained two pregnant females, and the other contained three pregnant females. A colony in South Carolina contained four pregnant females, the greatest of any colony sampled. The other colony in South Carolina contained two pregnant females. The colonies occurring in Mississippi and North Carolina contained two breeding females per colony.

Breeding females were represented in all age classes except for the 0- and 1- year age classes. The ≥5 year age class contained the greatest number of breeding females ($n = 54$); however, this class included individuals up to 18 years old. Based on true known female ages from cementum annuli analyses, mean breeding female age ranged from 5.0 (SE = 3.0) to 8.4 (SE = 1.3) in all seven states (Table 2), and the oldest recorded reproductively-active female was 18 years old. The 4-year age class contained the greatest number of breeding females for a single age class ($n = 18$). The largest number of breeding females in the ≥5-year age class occurred in females >10 years old and resulted in a greater number of breeding females for the collective age class ($n = 59$).

Discussion

Colony Composition

Overall, our study showed a range of colony sizes that encompassed reported sizes in both exploited and unexploited beaver populations outside of the southeastern United States. Three out of the seven states in our study had mean colony sizes similar to those reported from exploited populations outside the southeastern United States. In this study, Mississippi (5.1), North Carolina (5.53), and Virginia (3.75) mean colony sizes were very similar to reported mean colony sizes in Michigan (Bradt 1938; mean = 5.1), Alaska (Boyce 1974; mean = 4.1), and Ohio (Svendsen 1980; mean = 5.9); however, Alabama (7.75), Georgia (6.69), South Carolina (7.18), and Tennessee (8.0) mean colony sizes were similar to the studies in Nevada (Busher et al. 1983; mean = 8.2) and Massachusetts (Brooks et. al, 1980; mean = 8.1). The study sites in Nevada and Massachusetts were located in areas of limited to no public access. In both cases, trapping or hunting of beaver was prohibited; therefore both of the studies were conducted on unexploited beaver populations.

Sex Ratios

Previous research has suggested that per colony and per population sex ratios of beavers average near 1:1 (male:female) except for specific age classes. Dieter (1992) found that the sex ratios of beavers in eastern South Dakota were near 1:1 with a slight preference to males; however, he states that 65% of the 4.5–5+ age class were males accounting for a 1.24:1 sex ratio within that age class. Likewise, McTaggart and Nelson (2003) found that the sex ratio of 239 trapped beaver was 128:111 male to female, but 73% of adults were males. Our overall sex ratio of 1:1.1 was similar to other studies, slightly skewed towards males.

Age Structure

A 3-year mean age is associated with unexploited or lightly exploited populations (McTaggart and Nelson 2003). In contrast, heavily trapped nuisance beaver populations tend to exhibit lower mean age; for example, a heavily exploited beaver population studied in Wisconsin exhibited a mean age of 1.6 years (Peterson and Payne 1986). Zeckmeister and Payne (1998) conducted a study in central Wisconsin, in which a beaver population that had gone unexploited for 20 years was observed to decrease in mean age after the population was introduced to heavy trapping. Historically, all beaver populations sampled in this study have been trapped heavily, yet mean age is slightly higher than that described in these previous reports (in our study mean age of males = 2.0 + 0.3, mean age of females = 2.4 + 0.3).

Female Productivity

Most published literature on beaver defines a colony as a group of beavers occupying a single pond or stretch of stream, utilizing a common food supply, and maintaining a common dam or dams (Bradt 1938). Therefore, a typical beaver colony usually contains two breeding adults (a male and a female), their current offspring, and sometimes young from previous litters (Bradt 1938, Boyce 1974, Svendsen 1980, Busher 2007.) However, multiple lactating females have been documented to occur in the same colony, especially in areas that have high populations but lack optimal habitat. (Busher 2007). Some research suggests that beavers occurring in more linear habitats, such as river environments, tend to have fewer interactions with other colonies, whereas beavers inhabiting lacustrine habitats tend to have greater interactions with neighboring colonies (Crawford et al. 2009). These interactions have led to evidence of breeding between colonies and the presence of several productive females (Crawford et al. 2009). Three of the nine colonies exhibiting multiple pregnant females were associated with a river or stream system, but four were associated with wetlands surrounded by agriculture, development, or upland forest. Other than general habitat types, we have no estimates of habitat characteristics (i.e., quality, suitability, availability) and cannot test for these relationships.

Another reason that we may have encountered multiple lactating females within colonies could be explained by immigration. This would suggest that these sites of optimal habitat would provide some incentive for lactating females to quickly move into an area as soon as another lactating female is removed. While we cannot rule this out completely, we find it highly unlikely that females would abandon their colony site for another during kit-rearing. Furthermore, we reduced the chances for immigration by removing entire colonies as soon as possible. In most cases, our study observed mean trapping periods for multiple pregnant female colonies to be 13 days (SE = 6.26) which makes it less likely that pregnant or ovulating females dispersed into the area unless the habitat was associated with a river or stream system.

Management Implications

It appears the dynamics of beaver colonies may be more complex than earlier research has suggested and may have serious implications for managers when determining when to use lethal or non-lethal approaches to beaver management. In the southeastern United States, possible female philopatry may increase the reproductive potential of beaver populations. This reproductive potential accompanied by generally larger colony sizes found in this study and juvenile dispersal tendencies may prove detrimental to resources being protected in densely populated areas when left unexploited. Non-lethal management options, such as deep water fencing and water control devices, may be effective in deterring damage at a specific resource, but likely could prove detrimental to resources in the surrounding area if beaver populations remain unmanaged. Previous research has suggested that >3 beavers/colony need to be harvested to avoid saturated populations in the first year of management; a reduced harvest would be necessary to maintain a reduced beaver population (Zechmeister and Payne 1998). The beavers on our study sites were highly exploited, yet they still yielded older mean ages, colony sizes, and female productivity than more northern latitude studies experiencing similar conditions. Regularly used lethal control techniques will limit beaver numbers specific to the area experiencing beaver damage, while non-lethal management tools solely protect the resource. In some cases, it may be necessary to perform maintenance trapping at sites where non-lethal means are used to protect a resource. Our findings suggest that a manager should be aware of the individual dynamics of beaver populations in their area prior to management implementation.

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Literature Cited

Arner, D. H. and J. S. DuBose. 1982. The impact of beaver on the environment and economics in the southeastern United States. Transgressional International Congress of Game Biology 14:241–247.

Boyce, M. S. 1974. Beaver population ecology in interior Alaska. Thesis, University of Alaska, Fairbanks.

Bradt, G. W. 1938. A study of beaver colonies in Michigan. Journal of Mammalogy 19:139–162.

Brooks, R. P., M. W. Fleming, and J. J. Kennelly. 1980. Beaver colony response to fertility control: evaluating a concept. Journal of Wildlife Management 44:568–575.

Busher, P. E. 2007. Social organization and monogamy in the beaver. Pages 280–290 *in* Rodent Societies, J. D. Wolf, and P. W. Sherman, editors. The University of Chicago Press, Chicago, Illinois.

———, R. J. Warner, and S. H. Jenkins. 1983. Population density, colony composition, and local movements in two Sierra Nevadan beaver populations. Journal of Mammalogy 64:314–318.

Crawford, J. C., Z. Liu, T. A. Nelson, C. K. Nielsen, and V. K. Bloomquist. 2009. Genetic population structure within and between beaver (*Castor canadensis*) populations in Illinois. Journal of Mammalogy 90:373–379.

DeStefano, S., K. K. G. Koenen, C. M. Henner, and J. Strules. 2006. Transition to independence by subadult beavers (*Castor canadensis*) in an unexploited, exponentially growing population. Journal of Zoology 269:434–441.

Dieter, C. D. 1992. Population characteristics of beavers in eastern South Dakota. American Midland Naturalist 128:191–196.

Larson, J. S. and F. C. Van Nostrand. 1968. An evaluation of beaver aging techniques. Journal of Wildlife Management 32:99–103.

McNew, L. B., Jr.,.and A. Woolf. 2005. Dispersal survival of juvenile beavers (*Castor canadensis*) in Southern Illinois. American Midland Naturalist 154:217–228.

McTaggart, S. T. and T. A. Nelson. 2003. Composition and demographics of beaver (*Castor canadensis*) colonies in central Illinois. American Midland Naturalist 150:139–150.

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.

Svendsen, G. E. 1980. Population parameters and colony composition of beaver (*Castor canadensis*) in southeast Ohio. American Midland Naturalist 104:47–56.

Swafford, S. R. 2003. Population survey methods, immobilization approaches, and morphological charactristics for beavr in Lowwndes County, Mississippi. M.S. Thesis, Mississippi State University, Mississippi State.

Shwiff, S. and K. Kirkpatrick. 2008. Estimating the costs of beaver damage management in Mississippi. Report of USDA APHIS National Wildlife Research Center's Economic Program to USDA APHIS Wildlife Services, Starkville, Mississippi.

Van Nostrand, F. C. and A. B. Stephenson. 1964. Age determination for beavers by tooth development. Journal of Wildlife Management 28:430–434.

Woodward, D. K. 1977. Status and ecology of the beaver (*Castor canadensis carolinensis*) in South Carolina with emphasis on the Piedmont region. Thesis, Clemson University, Clemson, South Carolina.

Zeckmeister, M. T. and N. F. Payne. 1998. Effects of trapping on colony density, structure and reproduction of a beaver population unexploited for 19 years. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:281–291.