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Colony Composition and Demographics of Beavers in Illinois

Stanley T. McTaggart

Eastern Illinois University

This research is a product of the graduate program in Biological Sciences at Eastern Illinois University. Find out more about the program.

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Date
COLONY COMPOSITION AND DEMOGRAPHICS

OF BEAVERS IN ILLINOIS

(TITLE)

BY

STANLEY T. McTAGGART

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

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IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

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OF BEAVERS IN ILLINOIS

A Thesis Presented
by
STANLEY T. McTAGGART

Submitted to the Graduate School of
Eastern Illinois University
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of the requirements of the degree of
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ABSTRACT

Beavers (Castor canadensis) have been extensively studied throughout North America, but little research has been conducted on this species in Illinois and the Midwest. Beavers exhibit wide variations in colony composition and demographics over their broad geographic range, so regional research is important for sound management. The objectives of this study were to investigate the: (1) typical composition of beaver colonies in Illinois; (2) reproductive potential of female beavers in Illinois; (3) sex-age composition of beaver populations in Illinois; and (4) efficacy of night-vision surveys versus removal trapping for estimating colony size. This study was conducted during the 1999-00 and 2000-01 trapping seasons in central and southern Illinois. I harvested and aged 239 beavers (128 males:111 females). The average colony contained 5.6 beavers. Family groups consisting of a breeding pair and at least 1 offspring composed 86% of my colonies, while the other 14% consisted of only a breeding pair. An additional adult (≥2.5 years old) was found in 43% of the colonies. The sex-age composition of beavers taken from trapped-out colonies differed from that of beavers harvested by trappers. Trappers took significantly more yearling and 2.5 year olds, whereas more kits and older beavers were taken in trapped-out colonies. I did not find significant over-winter weight losses in kits, yearlings, or adults. The mean number of ova produced annually was 2.5, 3.6, and 4.4/female for 2.5 year olds, 3.5 year olds, and older females, respectively. Fetal rates were 3.0, 3.4, and 4.2/female for the 3 age-classes. In utero loss was estimated at 11%. Circumstantial evidence suggested that the presence of an older breeding adult female suppressed ovulation in subordinate females. I found no evidence that the presence of yearlings and subadults in a colony allows parents to raise more kits. Night vision surveys under-estimated the size of colonies, accounting for only 55% of the beaver present.
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INTRODUCTION

More research has been conducted on beavers (*Castor canadensis*) than on any other furbearer in North America, attesting to the ecological and economic importance of this species (Novak 1999). Beavers are important because they create and maintain wetland habitat, provide recreational opportunities for trappers and wildlife enthusiasts, and sometimes cause serious nuisance problems. Although the species has been studied extensively in Canada and some northern and western states, relatively little research has been conducted in the Midwest, including Illinois. The purpose of this study was to provide descriptive information on the composition and demographics of beaver colonies in Illinois. The work reported here represents part of a larger study conducted cooperatively by the Department of Biological Sciences at EIU, the Cooperative Wildlife Research Laboratory at SIU-C, and the Illinois Department of Natural Resources to monitor and detect changes in beaver populations statewide using helicopter surveys. The specific objectives of my study were to: (1) estimate the average size of beaver colonies in central and southern Illinois, (2) investigate the sex-age composition of colonies, (3) estimate the reproductive potential of beaver in Illinois, and (4) compare the relatively efficacy of two census methods (removal trapping and night-vision binocular censuses) for estimating colony size.
LITERATURE REVIEW

Historical Perspective

Beavers were historically abundant throughout the waterways of North America. In the 17th century the continental population was estimated at 60-400 million (Schulte and Muller-Schwarze 1999). However by 1850, populations had declined substantially throughout most of the range (Pietsch 1956, Novak 1999). The extirpation of beavers during the period of European settlement resulted from at least 3 factors: (1) heavy trapping pressure stimulated by the demand for pelts in Europe and the U.S., (2) the predominance of climax riparian habitats throughout much of the continent, which supported relatively sparse beaver populations, and (3) subsistence harvests of beavers by Native Americans for food (Novak 1999).

By the turn of the 20th century, only a few small populations remained east of the Mississippi (Schulte and Muller-Schwarze 1999). The last beaver reported in Illinois was harvested in 1912. Reintroduction efforts in Illinois began in 1929 and ended in 1938 with a total of 46 animals released in 4 counties. Iowa and Indiana were also reintroducing beavers at this time and the success of the beaver in Illinois was likely aided by immigration from neighboring states. By 1946, complaints from landowners resulted in the Illinois Department of Conservation (currently IDNR) translocating problem animals from these areas to suitable habitat in other areas of the state. The first legislated trapping season for beaver in Illinois took place in 1951 and resulted in a harvest of 659 animals. Trappers were limited to 10 beaver and the average pelt price was $7.48 (Pietsch 1956).

The fur market collapsed in the 1980’s resulting in fewer active trappers and a decrease in annual beaver harvests (Novak 1999). This resulted in expanding beaver populations across
much of the Midwest (Dieter 1992, Novak 1999). In addition, urban expansion and the improvement of streams and riparian habitats in many suburban areas brought beavers and humans closer together, resulting in more frequent nuisance complaints. Today, the damages caused by beavers flooding roads, crops and timber and chewing on timber and ornamental plantings (estimated at $75-$100 million annually in the U.S.) exceeds the economic value of pelts (Novak 1999). In Illinois, permits issued to landowners by the IDNR for the removal of nuisance animals have increased from 250 in 1985 to 942 in 1999 and beavers ranked as the third most common nuisance species (Bluett 2000). The average yearly harvest in Illinois over the 25-year period from 1975 to 1999 was 4,400 beavers with an average pelt price of $8.00 (R. Bluett, IDNR, pers. comm.). Trapping records show that more beavers are harvested annually today than during the height of beaver exploitation in the 18th century and yet because of limited habitat and increasing nuisance complaints, many biologists consider beavers to be under-harvested in many locations (Novak 1999).

Monitoring Beaver Populations

Monitoring population trends is an important component of wildlife management, particularly for those species that are harvested as game and/or nuisance animals. Beaver populations are typically monitored using (1) surveys of trappers and annual harvests, (2) annual counts of beaver sign (e.g. lodges, food caches, or tracks) along aerial or ground transects, and (3) estimates of mean colony size, in conjunction with aerial colony surveys, to estimate population size. Managers in Illinois currently rely on harvest surveys (Bluett and Hubert 1991), trapper surveys (Anderson and Campbell 1998), bridge track surveys (Bluett 2001), and the number of nuisance permits issued (Bluett 1998) to monitor beaver trends. There are advantages
and disadvantages of each technique and many wildlife agencies use a combination of these to monitor beaver populations.

The most common method of monitoring beaver populations is to survey annual trapper harvests. All 15 states and Canadian provinces in the North Central Section of The Wildlife Society use harvest surveys to develop management recommendations (Clark and Andrews 1982). These surveys are relatively inexpensive and easy to implement. However, the accuracy of surveys is low due to the close correlation between trapper effort and fur prices (Peterson and Payne 1986). Pelt prices may influence harvests to a greater extent than population size (Hill 1982). In addition, the sex-age composition of the population and of individual colonies may be misrepresented in these surveys because trappers are likely to target larger and more profitable beavers (Larson 1967, Clark and Andrews 1982). However, Novak (1977) found no bias in trapper harvests and concluded that the age distribution of the trapped sample was representative of the actual age distribution of the population.

Population indexes based on surveys of beaver sign (lodges, food caches, or tracks) are usually more costly to obtain and are influenced by such factors as weather conditions, visibility, experience of the observers, and (in the case of lodge counts) the mean size of the colony (Clark and Andrews 1982). However, the value of colony counts can be greatly improved if the mean size, composition and demographics of beaver colonies are known for populations inhabiting different regions or habitats (Robel and Fox 1993). To estimate colony size and composition, removal trapping is commonly used and is thought by be more accurate and expedient than live trapping (Hay 1958, Busher et al. 1983). Peterson and Payne (1986) used data from completely trapped nuisance colonies to determine the average number of beavers/colony in Wisconsin. Other researchers have used night-vision binoculars to survey the number and age composition of
beavers in representative colonies (Svendsen 1980, Easter-Pilcher 1990, Osmundsen and Buskirk 1993). Like most ocular surveys however, these can be affected by differential activity levels of the sex-age classes, visibility, and the experience of the observers (Lancia et al. 1994).

Beaver are reported to vary geographically with regard to colony size (Novak 1999), body mass, and litter size (Hill 1982). In addition, they are common throughout Illinois but are not uniformly distributed and their relative abundance in different regions of the state is poorly understood. This variation suggests that the responsible management of statewide beaver populations requires current information on the composition and demographics of regional populations. This thesis represents a contribution to this base of information.

METHODS

I trapped beavers from December to March during the 1999-2000 and 2000-01 trapping seasons. The colonies were located in south-central Illinois on private, state or federal lands. The colonies were located by searching rivers and lakes by boat and on foot, and by referrals from landowners and IDNR staff. Beavers were trapped using #330 and #280 conibear (body-gripping) traps, #5 double long-spring leghold traps or cable snares. I set traps on or near lodges, bank dens, dams, food caches, feeding stations, and scent mounds using either castoreum-based lures or food lures. The incidental catch of state-endangered river otters (Lutra canadensis) was reduced by avoiding indiscriminant sets in travel channels (Sullivan 1999) and by modifying the triggers on the #330 conibear traps (Gotie et. al. 2000). Colonies were trapped until there was no sign of activity for one week (such as fresh tracks or cuttings, dam repairs or fired traps).

In addition to these beavers, I solicited beaver carcasses from cooperating trappers in central and southern Illinois. Because these animals were taken from colonies that were not
completely trapped out, the sex-age composition of this sample was not necessarily representative of the whole population. Consequently, I used the data from these solicited animals to assess age-specific body weights and reproductive rates, but excluded them when estimating the mean size and sex-age composition of colonies.

Each trapped beaver was marked with a zinc tag containing a unique identification number designating the colony from which it was caught and the date of capture. This identification number stayed on the carcass from the time of capture through dissection. I weighed each beaver on a 50 kg spring scale, which was accurate to 0.5 kg. Beavers were then skinned, weighed again (to assess skinned weight) and then dissected to collect organs. Lower jaws were removed from each beaver for aging and complete reproductive tracts (ovaries, oviducts, uteri, and cervixes) were collected from each female to assess age-specific reproductive performance.

I labeled each lower jaw with an identification tag and placed it in a nylon mesh bag, then boiled it for approximately 2.5 hours to loosen teeth. All 4 cheek teeth (1 premolar and 3 molars) from the left side of the lower jaw were individually labeled, then removed for aging. The removal of teeth usually required cracking the jaw in several places with a hammer and chisel. Beavers were aged based on the eruption, degree of basal closure and deposition of cementum annuli on these cheek teeth (Van Nostrand and Stephenson 1964, Larson and Van Nostrand 1968). Based on these ages, I estimated the sex-age composition of each colony and of the total sample captured during this study.

Reproductive tracts from female beavers captured during the 1999-2000 season were cleared prior to counting placental scars. Clearing was accomplished by first fixing the tract in Mossman’s AFA (30 parts 95% alcohol, 10 parts formalin, 10 parts acetic acid and 50 parts
distilled water), blotting it dry, then bleaching it in hydrogen peroxide and clearing it with methyl salicylate (Provost 1962, Henry and Bookhout 1969). This process was reported to darken placental scars and enhance scar visibility. However, I found scars to be more visible in fresh tissue. Consequently, during the 2000-2001 season, I removed the ovaries and stored them in AFA solution, but froze the rest of the tract for subsequent examination. After the trapping season ended, I thawed each uterus, split it lengthwise with scissors, and examined each horn for placental scars. Scars in these fresh, unstained tracts generally were more evident than in the cleared tracts. In some cases, a light was held behind the uterus to better distinguish the dark placental scars. It was also helpful to palpate for scars by passing the tissue between the fingers, down the length of each uterine horn, feeling for thicker sections of tissue (Hodgdon 1949, Brenner 1964). Visible embryos were counted and the crown-rump length of each embryo was measured in mm to estimate age (Bond 1956). Placental scar counts and embryo counts were used to estimate the past and current year’s reproductive success, respectively (Bond 1956, Brenner 1964).

Ovaries were examined macroscopically by longitudinally cross-sectioning each ovary into sections approximately 2mm thick (Provost 1962, Henry and Bookhout 1969). Corpora lutea were distinguishable as whitish bodies against the gray background of the ovary (Provost 1962). I compared the number of corpora lutea in each tract to the number of embryos (when these were visible) to estimate in utero losses. Since relatively few females contained visible embryos, the counts of corpora lutea provided a much larger sample from which to estimate age-specific reproductive performance (Provost 1962, Brenner 1964, Henry and Bookhout 1969).

To provide a second estimate of the number of beaver in each colony, I conducted nocturnal censuses at a subsample of my study colonies prior to removal trapping. These counts
were conducted using night-vision binoculars to observe colonies in both riverine and lacustrine habitats. Each colony was observed 1 or 2 times by an experienced observer for ~2.5 hours following sunset. The observer sat ~10 m downwind from the lodge or bank den wearing camouflage clothing. We counted each beaver as it emerged from the lodge and moved about the cache and surrounding area. Only beaver that could be positively identified as unique individuals were counted to avoid overestimating colony size. The sound (hissing, whining, chewing) of beavers still present in the lodge was recorded as an individual, if heard while other beaver were in view. The highest count was used to estimate colony size when 2 observations resulted in different estimates of colony size. After removal trapping was completed at each colony, I conducted a final nocturnal observation to ensure that no beaver remained at the site.

The non-parametric binomial test was used to test whether the observed sex-ratios of beavers differed from an expected ratio of 1:1 (Sokal and Rohlf 1995). A X² test was used to test whether age-class frequencies were different for beavers harvested from my research colonies and those harvested by cooperating trappers. Differences between the mean ages of beavers harvested by trappers and those collected from research colonies were tested using a 2-sample t-test. A one-way ANOVA was used to test whether mean colony size differed among colonies inhabiting rivers, lakes, and ditches. Differences in the mean number of ova produced per female in the yearling, 2.5, and ≥3.5 year old age classes also was tested using ANOVA. The correlation between the number of auxiliary beavers in a colony and the number of kits raised was tested with the product-moment correlation coefficient. This test was also used to examine the correlation between the number of beavers observed during nocturnal censuses and the number actually present in the colony. All analyses were conducted using the SAS statistical package (SAS Institute Inc., Cary, NC).
RESULTS

Sex-Age Composition of Beaver Populations

A total of 239 beavers was harvested during this study, including 169 that I harvested and 70 supplied by cooperating trappers. The sex ratio of this sample (128 males:111 females) did not differ from unity (P = 0.301). Males composed 53-55% of the kit, yearling and adult age classes. Ages ranged from 0.5 to 15.5 years old; however, 74% were ≤ 2.5 years of age (Fig. 1). The age distribution of beavers harvested from my trapped-out research colonies differed from those supplied by cooperating trappers ($X^2 = 25.7; 15$ df; $P = 0.04$). Cooperators harvested relatively more yearling and 2.5 year old beavers (58.6%) and fewer older beavers (10.0%), whereas these classes comprised 34.3% and 34.0%, respectively, of the beavers in my research colonies (Fig 2). The mean age of beavers taken from the research colonies was 2.8 years, whereas the mean age of beavers taken by trappers was 2.1 years ($t = 1.82; 202$ df; $P = 0.07$). The mean age of all beavers from both samples was 2.7 years.

Colony Size and Composition

I attempted to trap-out 54 individual colonies during the 2 trapping seasons and succeeded in trapping-out 28 colonies. Of these 28 colonies, 14 (50%) were located in riverine habitats, 9 (32%) were in lacustrine habitats, and 5 (18%) were in drainage ditches. Individual colonies ranged in size from 2 to 11 beavers. The mean number of beavers per colony was 5.6 (SD = 2.5). Colony size did not differ for beavers inhabiting the 3 habitats ($F = 1.54, 2$ df, $P = 0.234$), averaging 4.0, 5.6, and 6.3 beavers/colony in ditch, riverine and lacustrine habitats, respectively. A typical colony was composed of 2 breeding adults, 1-2 yearlings, and 2 kits (Fig. 6). However, 43% (12/28) of these colonies had at least 1 additional adult (≥2.5 years old)
resident in addition to the breeding pair. I found no correlation between the number of auxiliary "helpers" (resident yearlings and non-breeding adults) in a colony and the number of kits raised in the colony ($r = 0.23, P = 0.395$).

**Reproductive Rates among Female Beavers**

Of 111 female beavers examined, 35 (31.5%) were kits that lacked indications of sexual maturity (mature follicles or corpora lutea) (Table 1). Only 2 (7.4%) yearling females had ovulated and 1 of these individuals carried 3 fetuses. The percentage of females ovulating increased to 52.6% among 2.5 year olds and 76.6% among beavers ≥ 3.5 years (Table 1).

Ovulation rates, for those females that ovulated, did not differ among age classes, but the tendency was for older females to produce more ova, increasing from 2.5 ova/female in yearlings to 3.6 in 2.5 year olds and 4.4 in older females ($F = 1.34; 35 \text{ df}, P = 0.28$; Table 1). Relatively few females ($N = 22$) were captured late enough in the breeding season to carry fetuses. Of those that did, the mean number of fetuses per pregnant female was 3.0 for yearlings, 3.4 for 2.5 year olds, and 4.3 for beavers ≥3.5 years old ($F = 0.75; 21 \text{ df}, P = 0.486$; Table 1). The number of placental scars/female for all females in each age-class was influenced by age ($F = 19.91; 73 \text{ df}; P = 0.001$). Females that were 2.5 years old averaged 1.3 scars, 3.5 year old females averaged 2.0 scars, and older females averaged 3.3 scars. There was a positive correlation between the weight of the mother and the number of ova shed ($r = 0.635; P = 0.001$) for all females. However, when this relationship was addressed separately for females in each age-class, body weight influenced ovulation rate in 2.5 year olds ($r = 0.476; P = 0.03$), but not in older females ($r = 0.323; P = 0.12$).

**Fertilization Rates and Prenatal Mortality**
I estimated the percentage of ova that undergo fertilization and early development using age-specific ovulation rates and fetal rates. Twenty-two females in the older age-classes produced 97 ova and carried 88 fetuses, suggesting that 91% of the ova produced are fertilized and implant. Of the fetuses I examined, 4 (4%) were in the process of being resorbed. Consequently, the loss of ova and early embryos was approximately 13%.

**Age-Specific Mortality and Life Expectancy**

Based on the ages of the breeding females in the 28 study colonies and age-specific fetal rates, I estimated that these colonies should have produced approximately 110 kits at birth. However, during the winter I found only 47 kits in these trapped out colonies. Therefore, it appears that the mortality rate of kits during the perinatal period and first 6 months of life may be as high as 57%. Using this estimate in conjunction with the age-structure of the 134 beavers that were trapped and aged from these colonies, I constructed a life table for these animals (Table 2). Age-specific mortality rates \( q_x \) were highest during the first 6 months of life, then remained relatively constant from 0.5 to 2.5 years old. Assuming that the age-structure of this population is stable, approximately 34-40% of the animals in each of these age-classes died each year. Annual mortality rates generally were lower for older beavers and were lowest for 4.5 year olds. The life expectancy \( e_x \) of beavers at birth was approximately 2 years (Table 2).

**Body Weights**

Whole body weights ranged from 3.2 to 32.3 kg. Mean weights were 8.9 kg, 13.5 kg, 17.7 kg, and 22.3 kg for kits, yearlings, 2.5 year olds, and ≥3.5 olds, respectively (Table 4). Whole body weights differed among age classes \( (F = 316.8, 196 \text{ df}, P = 0.0001) \), but did not differ between sexes \( (F = 0.5, 1 \text{ df}, P = 0.466) \). Skinned weights and whole weights were highly correlated \( (r = 0.98, P = 0.0001) \), with the pelt accounting for approximately 25% of the whole
body weight. Based on 182 beavers for which I recorded both whole and skinned weights, the linear relationship between these measurements (kg) was described by the equation:

\[ \text{Whole weight} = 1.3 \times \text{(skinned weight)} + 0.3 \]

I found no evidence that beavers in central and southern Illinois lose weight as winter progresses. There was no weight change among kits (\( r = 0.11, N=59, P = 0.42 \)), yearlings (\( r=-0.17, N=44, P=0.267 \)), or among older beavers (\( r = -0.19, N=93, P = 0.07 \); Figs. 3, 4, 5).

**Comparison of Nocturnal Censuses and Removal Trapping for Estimating Colony Size**

The 28 colonies that I trapped-out required an average of 24.4 trap-nights/colony to remove all beavers. Across all 3 habitat types, beavers were trapped at a rate of 7.6 trap-nights/beaver. Nocturnal censuses with night-vision binoculars were conducted at 16 colonies that were subsequently trapped out. With 1 exception, I underestimated the actual size of each colony during these censuses. The mean number of beaver observed per colony was 2.9; the mean number actually present was 5.3. Therefore, night-vision censuses accounted for only about 55% of the beavers present. Furthermore, the discrepancy between the estimated and actual number of beaver in a colony tended to be greater for bigger colonies (Fig 7). However, a strong positive correlation was found between the number of beavers observed during these censuses and the number present in the colonies (\( r= 0.80; P=0.001 \)). Based on my censuses at these 16 colonies, the number of beaver present in a colony can be estimated from the equation:

\[ \text{No. of beavers in colony} = 1.33 \times \text{(maximum no. observed)} + 0.5 \]
DISCUSSION

Sex-Age Composition of Beaver Populations

Beavers on my study areas exhibited an overall sex ratio close to 1:1, which is typical of most beaver populations. Hill (1982) and Novak (1999) reviewed sex ratios in samples collected across the species' geographic range and concluded that ratios were approximately equal in most areas. They noted that when the sex ratio in a sample differed significantly from equality it was likely due to small sample size, trapping bias, and/or random local differences in fertilization. However, sex ratios may be skewed within particular age-classes. Males predominated in all age classes through 3.5 years of age on my study area. Others have reported that males often outnumber females only in the kit and yearling classes, whereas older age-classes are skewed towards females (Osborn 1953, Hendry 1966). Woodward (1977) reviewed age-specific sex ratios from 15 studies and reported male:female ratios of 111:100 among juveniles and 91:100 among adults. Higher proportions of males at birth may be an adaptive mechanism to offset higher mortality rates experienced by dispersing yearling and 2-year old males, ensuring an operational sex ratio near unity. However, specific research supporting this hypothesis is lacking (Novak 1999).

The apparent age structure of beaver populations may be biased by the method, location, duration and intensity of trapping. For example, relatively unbiased samples are more common when the entrances to lodges and dens are trapped intensively using submerged conibear sets. However, snares and leghold traps set on land near scent mounds or dams are more likely to capture adults (Hill 1982). The natural age structure attained by beaver populations is probably
best obtained by trapping out previously unexploited colonies (Hill 1982). Based on this assumption, I believe that the age structure of the beavers that I harvested from the 28 trapped-out research colonies provides a reasonable estimate of the structure of unexploited or lightly exploited beaver populations in Illinois.

Although 74% of the beavers that I collected were \( \leq 2.5 \) years old, a number of old beaver were present in the sample, including 7 individuals > 10 years old. Beavers in the wild typically do not exceed 10 years of age, however, individuals as old as 21 and 24 years have been harvested (Larson 1967, Brown 1979). The percentages of kits, yearlings and adults in my trapped-out colonies (31%, 20%, 49%) were similar to the composite percentages of these age-classes from 10 previous studies (30%, 23%, 47%) reported by Hill (1982).

The sample of beavers provided to me by commercial trappers contained a higher percentage of yearlings and 2.5-year olds than my trapped out colonies. This difference may have occurred because trappers tended to set traps at sites frequented by dispersing subadults. Most of our cooperators concentrated their trapping effort during the spring dispersal period and few attempted to trap all of the beavers from any colony. The difference may also reflect the past history of trapping at beaver colonies. Cooperating trappers tended to trap a few animals from the same areas each year, which is likely to truncate the older classes, leaving predominantly yearlings and 2.5-year olds. The literature seems to corroborate the latter hypothesis. The colonies that I trapped out represented unexploited or lightly exploited populations which were either located on public land where trapping generally is prohibited or on private land which was rarely trapped. The mean age of beavers taken from heavily trapped nuisance colonies in Wisconsin was 1.6 years (Peterson and Payne 1986), whereas the mean age of beavers from
unexploited or lightly exploited populations have ranged from 2.6 years in Ohio, to 3.0 years in Alaska, to 3.8 years in Newfoundland (Henry and Bookhout 1969, Boyce 1974, Payne 1982).

**Colony Size and Composition**

The mean colony size (5.6) in this study is in the middle to upper range of reports from across North America (Table 5). Others have reported mean colony sizes ranging from 3.2 in New Brunswick to 8.2 in Nevada (Nordstrom 1972, Busher et al. 1983). In other Midwestern studies, colonies averaged 5.1 beavers in Michigan and 5.9 in Ohio (Bradt 1938, Svendsen 1980). The largest colony reported was 12 in Michigan, similar to the colony of 11 that I found on the Embarras River. The latter colony was in prime habitat and had not been trapped in recent years.

Molini et al. (1981) estimated that 20% of a beaver population was made up of “floaters” that have not found a mate or established a territory of their own. These individuals may move into an established colony after one or both adults have been removed, thereby inflating the apparent size of the colony. The apparent size of a colony could also be biased if a breeding adult or subadult abandoned a lodge after the removal of a mate or parent (Svendsen 1989). Thus, it is possible that I overestimated or underestimated the size of individual colonies by including non-resident “floaters” or by missing early dispersers. However, since most of my trapping was done under ice when most colonies were closed to dispersal and biases associated with immigration or emigration are offsetting, I do not believe that they significantly influenced my estimate.

The mean size of colonies did not differ significantly among the 3 different habitat types (river, lake and drainage ditch), but the trend was for drainage ditches to have fewer beavers per colony and lakes to have the most. These results are consistent with the observation that
dispersing yearlings and young adults are pushed into unoccupied and marginal habitats.

Generally, optimal habitats provide an abundance of preferred woody winter foods, whereas those lacking these resources are considered to be poorer habitat (Hill 1982). The quality of habitat is known to influence litter size, colony size and composition (Huey 1956, Gunson 1970).

Drainage ditches in Illinois appear to provide suboptimal beaver habitat. These ditches drain large agricultural fields and are quickly flooded with heavy rains, whereas summer droughts may dry them completely. In addition, woody vegetation, an important source of winter food and building material, is sparse because many landowners cut brush regularly to maintain flow in these ditches. Consequently, it appears that beaver colonies inhabiting ditches may be smaller than those inhabiting other habitats.

Twenty-four of the 28 colonies (86%) that I trapped out contained a breeding pair plus at least one offspring (“family colonies”) and the remaining 4 colonies contained a pair of adults without offspring (“pair colonies”). I did not find any single animal colonies or “bachelor beaver” in this study. Peterson and Payne (1986) trapped out 42 nuisance colonies in Wisconsin and found 65% family colonies, 19% pair colonies and 16% singles or bachelor beavers.

The high percentage (43%) of colonies that contained at least one additional adult on my study area is consistent with the hypothesis that beaver populations in central Illinois are at high densities relative to the amount of available habitat. Muller-Schwarze and Schulte (1999) reported that 22-88% of the colonies studied in high density populations have an additional adult present. This is likely due to a lack of suitable, unoccupied habitat, which discourages dispersal (Hill 1982, Zeckmeister and Payne 1998). In contrast, low-density populations were reported to have an additional adult present in 0 to 13% of the colonies (Muller-Schwarze and Schulte 1999).
Bush and Lyons (1999) noted that delayed dispersal can occur when populations are high and available habitat is saturated, or at lower densities when no quality habitat is available.

Auxiliaries contribute to the maintenance of the lodge and dams, cooperate in collecting material for the food cache, and help to feed and care for kits (Hodgdon and Lancia 1983, Novak 1999). Therefore, I hypothesized a positive correlation between the number of auxiliaries and the number of kits in beaver colonies. Kin selection theory suggests that it may be adaptive for sexually mature offspring to stay in the family group and help parents in raising kits if these auxiliaries increase their indirect fitness by augmenting the reproductive success of their parents or their direct fitness by gaining familiarity with the skills of parenting (Hamilton 1963, Feldhamer et al. 1999). For example, Moehlman (1979) showed that among black-backed jackals (Canis mesomelas) the number of young that survive is directly related to the number of auxiliaries in the family. Approximately 1 additional pup can be raised for each auxiliary jackal. In contrast, I found no evidence that auxiliaries increase the reproductive success of their parents. This is consistent with Smith's (1997) conclusion that auxiliaries did not increase reproductive success in beaver colonies in northern Wisconsin and Minnesota. However, it is possible that these subadults increase their chances of breeding successfully in the future by gaining familiarity with parenting, maintaining caches and lodges (or bank dens) and the home territory (individual selection). Further, as suggested previously, yearlings and young adults living in high density populations may increase their chances of survival by staying with their parents where there is little chance of finding a suitable, unoccupied territory (Heske and Bondrup-Nielsen 1990).

Reproductive Rates among Female Beavers

The breeding season for beavers living at northern latitudes runs from December through March (Brenner 1964, Bergerud and Miller 1977, Svendsen 1989), however in the central and
southern U.S. breeding starts earlier and the season can extend from October through March (Hill 1982, Novak 1999). Beavers are polyestrous and will enter estrous repeatedly every 14 days until bred. Doboszynska and Zurowski (1983) estimated that 16% of captive European beavers (Castor fiber) were successfully bred on the first attempt. If North American beavers are similar, it may take several weeks or months for a receptive female to successfully breed. The majority of females in my sample were trapped in January and February, which was late enough in the reproductive season for most of these females to have ovulated and bred. Nevertheless, my estimate of the proportion of females that breed annually is likely to be conservative because some females harvested early in the trapping season probably would have ovulated and bred later in the season.

My data are consistent with other reports showing that female beavers are not sexually mature until they are at least 1.5 years old (Hill 1982, Novak 1999). Further, yearlings do not typically breed in most populations and contribute little to a population’s overall production. I found only 2 (7%) reproductively active yearlings and both were from heavily exploited populations trapped annually by cooperating trappers. Muller-Schwarze and Schulte (1999) noted that yearling beavers are more likely to reproduce in exploited populations. When beaver populations are harvested, adult survivorship decreases which vacates territories and enhances survivorship and reproduction of dispersing yearlings and subadults (Boyce 1981). Deiter (1992) found no reproduction by yearlings in a lightly trapped sample from South Dakota. However, Peterson and Payne (1986) found 13% of yearlings bred in nuisance colonies that were trapped regularly. The highest percentage of breeding yearlings (44%) was reported by Lyons (1979) for beavers in Massachusetts.
Litter size is influenced by the age and the nutritional status of females (Gunson 1970, Wigley et al. 1983). Age-specific ovulation rates for beavers in Pennsylvania were reported as 4.0 ova/female in 2.5 year olds and 6.6 ova/female in older individuals (Brenner 1964), whereas Henry and Bookhout (1969) found rates of 3.5, 4.0, and 4.6 ova/female in yearlings, 2.5 year olds, and older females, respectively, in Ohio. Among the beavers in my sample, fecundity increased with age through the first 4 years of life. However, ovulation rates were somewhat lower than those reported by others. Since, fecundity in beavers is thought to be negatively correlated with population density (Boyce 1974, Payne 1984), this is perhaps another indication that the beavers on my study areas were at relatively high densities.

The quantity and quality of food available to females generally affects reproductive rates in beavers. My results are consistent with several previous studies that have found a positive correlation between a litter size and the weight of the mother (Henry and Bookhout 1969, Boyce 1974, Wigley et al. 1983). Some authors have suggested that the cost of a large litter one year leads to a smaller litter the next year (Smith and Jenkins 1997, Ruusila et al. 2000). Presumably the energetic costs of gestation and lactation deplete a female’s energy reserves leading to a smaller litter the subsequent year.

Schulte and Muller-Schwarze (1999) noted that pheromones of dominant females apparently suppressed ovulation in subordinate females. Though this phenomenon was not tested directly, I found some support in my trapping records. I caught 8 sexually mature (2.5 or 3.5 year old) female beavers at colonies where an older, pregnant female had already been removed. Five of these were trapped within a week after the dominant female had been removed and none of these subordinates had ovulated. However, in each of the other 3 cases, when the dominant female had been trapped >2 weeks earlier, the subordinate had ovulated. It is possible that these
younger females were early dispersers who had emigrated into the colony after the removal of the dominant female. Svendsen (1989) reported that some adults and even entire colonies move to a new location after the loss of a mate, but it was more common for beavers to remain at the lodge and wait for a new mate. Since ice cover was present for most of the trapping season, minimizing the chance of dispersal, it is more likely that these cases were subordinate auxiliaries that ovulated after the removal of the dominant female.

**Fertilization Rates and Prenatal Mortality**

Some of the ova shed are not fertilized, some fertilized ova do not implant, and some embryos are resorbed during development (Provost 1958, Henry and Bookhout 1969). Collectively, these losses constitute pre-natal mortality and they cause actual reproductive rates (number of young born per female) to be lower than ovulation rates. Previous studies have shown that the mean number of embryos/breeding female tend to be low for beaver in California and some southern states, but higher in the Midwest. Four previous studies in the Midwest have reported mean fetal rates between 3.7 and 4.0/female, which is consistent with my estimate for beavers in Illinois (Table 7). In a review of previous studies, Novak (1999) reported that prenatal mortality can be high in beavers with pre-implantation losses ranging from 3.8% to 38.2% and post-implantation mortality adding another 2.7-17.2% loss.

In the only other Midwestern study to report prenatal mortality, Henry and Bookhout (1969) found that 16% of ova were lost prior to implanting and 7.2% of embryos were resorbed or lost. My estimate of 13% prenatal mortality should be considered conservative in that it covers only losses prior to March (early gestation), the time that I stopped collecting females.

**Age-Specific Mortality and Life Expectancy**
The life table can be a useful tool for estimating patterns of mortality and survival in a population. A static life table can be constructed from the age distribution of a standing population, if you assume that the differences in the numbers of animals in successive age classes are due to mortality (Molles 2002). Other assumptions for deriving valid estimates of population parameters from a life table are that: (1) the population is closed to immigration and emigration, (2) the population is stable, that is age-specific survivorship and reproduction are constant, (3) aging techniques are accurate, and (4) an unbiased sample of the standing population is aged (Caughley and Sinclair 1994, Molles 2002). These assumptions are often violated in wildlife populations and may not apply to the beavers that I studied (Caughley 1977). However, I am reasonably confident that the methods I used to sample and age the standing population reduced the probability of violating the third or fourth assumptions. Complete removal trapping of colonies avoids the bias towards larger adults which is common in many trapping studies (Buckley and Libby 1955). The populations that I studied were not closed, particularly because spring dispersal by yearlings and 2.5 year olds is common. But, immigration and emigration may be offsetting among colonies (Larson 1967). Finally, I do not know whether these populations were stable, but the high proportion of adults that I found in my population is typical of stable beaver populations (Boyce 1974, Busher 1987). Therefore, the life table that I calculated may be a useful tool for assessing mortality patterns in these lightly exploited colonies, but should be viewed with some caution.

The most striking result of the life table analysis is that the mortality rate from the fetal stage through the first 6 months of life appears to be relatively high (57%). This is in contrast to prior studies that have concluded that infant mortality is low in beavers. Novak (1999) cited several studies that estimated post-natal and juvenile mortality rates to be <10%, but also
reported several studies that found first-year mortality rates ranging from 19 to 52%. For example, Payne (1984) estimated a mortality rate of 52% for Newfoundland beavers from the embryo stage through the first 6 months of life. He could not account for this high rate and noted that it may have been artificially high because trappers were restricted to 1 beaver/colony and may have discarded kits. Female beavers on my study areas appeared to be in good condition and the winters were relatively mild, so it is unlikely that severe weather or starvation caused these losses. Regardless of the cause of mortality, the apparent number of surviving kits per colony was 1.7, which is similar to the rate of 1.3 kits/colony reported for beavers at or near carrying capacity (Taylor 1970 in Busher 1987).

Age-specific mortality rates appear to be higher for yearling and 2.5 year olds, relative to older adults. This outcome makes sense, as beavers disperse at these ages and mortality rates for dispersers are often high (Woodward 1977). In Ohio, first year mortality was estimated as 42% (Henry and Bookhout 1969). Bergerud and Miller (1977) reported that annual mortality averaged 46% in kits, yearlings, and 2-year-olds, then dropped to 12% in older beavers in Newfoundland. These estimates are similar to mine, which averaged 42% in the 3 youngest age classes and 17% among older beavers. It should be noted however, that dispersing yearlings and subadults often live as singles and pairs in bank dens that are difficult to detect. Therefore, these age-classes may have been under-estimated in my trapped sample and their mortality rates may be over-estimated (Molini et al. 1980).

Body Weights

The body weights of beavers vary with age, season, region, and food availability (Hill 1982). Beavers generally reach their full adult size by 3.5 years of age (Aleksiuk and Cowan 1969). Hill (1982) noted that the largest beavers in North America appear to be produced at mid-
continent, in the central and northern U.S. Most individuals are relatively lean through summer, then deposit body fat through the autumn. Throughout the northern extent of their range, beavers typically lack adequate food reserves during the winter to balance energy expenditures. Consequently, they use stored fat reserves and the food cache as energy sources and reduce heat and energy losses using the insulation provided by their fur and lodges, huddling, and metabolic depression. These adaptations are apparently quite effective as starvation is uncommon in beaver populations (Novakowski 1967).

The weights of beavers harvested during my study were generally higher than those reported in the literature. However, there are surprisingly few studies that have reported body weights during the last 30 years. This is probably because beavers have been aged based on dental characteristics rather than body weight since the 1960’s (Van Nostrand and Stephenson 1964, Larson and Van Nostrand 1968). Nevertheless, knowing the weights of beaver in each age-class may be useful for estimating the ages of live beavers when it is not possible to remove teeth and for comparing the condition of populations from the same region. Muller-Schwarze and Schulte (1999) reported the mean weights of kits, yearlings, 2-year olds and adults (≥3.5) from New York as 6.0, 9.0, 13.0 and 18.5 kg, respectively. Novakowski (1967) reported a mean winter weight for adults of 20.8 kg in Saskatchewan. For comparison, the mean weights of beavers in my study were 20-50% heavier than those in New York and adults were 7% heavier than adult beavers in Saskatchewan.

The large size of beavers in Illinois may be attributable to 2 factors. First, beavers can supplement their natural diet during the autumn with high quality agricultural crops, particularly corn and soybeans. It was common to see corn stalks with ears included in the food caches. Second, beavers on my study areas did not lose weight through the winter as is typical of beavers
at more northern latitudes (Novakowski 1967, Aleksuik and Cowan 1969, Smith and Jenkins 1997). I did not find a significant weight loss in adults or yearlings over winter, nor did kits show significant weight loss or gain. Weight losses in the north are attributable to the severity of the winters, prolonged ice cover, and shortage of quality food at those latitudes. We have milder winters in central Illinois. Although beavers were subjected to about 2 months of ice cover each winter, they probably do not experience significant food stress during this season.

Pelts accounted for about 25% of the total body weight of my beavers, regardless of age. This estimate should allow managers and other researchers to compare the skinned weights and whole body weights of beavers harvested in different studies or regions of Illinois.

Comparison of Nocturnal Censuses and Removal Trapping for Estimating Colony Size

Several studies have used nocturnal censuses with night vision binoculars to estimate beaver colony size (Osmundsen and Buskirk 1993, Easter-Pilcher 1990, Svendsen 1980). However, none tested the accuracy of these censuses by using colonies where the true composition was known and no effort was reported to measure their accuracy using a second independent method to validate their counts. Easter-Pilcher (1990) reported that she was able to distinguish kits, yearlings and adults using night vision scopes, but I was not confident assigning age-classes to beavers observed at night. Environmental conditions including wind and ice cover sometimes precluded censuses. Winds over 10 km/hr caused ripples and waves that made viewing swimming beaver very difficult on rivers and lakes under a tree canopy. The appearance of additional beaver after I was detected (and a tail-slap warning was given) was rare. The night vision optics were most effective in areas with little canopy cover and during brighter phases of the moon.
Wildlife managers often estimate the abundance and population trends of beavers by conducting aerial counts of lodges and/or food caches then multiplying these counts by mean estimated colony size to derive population size (Bergerud and Miller 1977, Peterson and Payne 1986). This method assumes that the mean size of colonies is consistent both spatially and temporally. But, Swenson et al. (1983) found this assumption to be invalid, reporting that cache counts did not correlate well with population size because mean colony size changed from area-to-area and year-to-year. These authors noted that the sex-age composition and age-specific natality of colonies must be examined periodically if beaver are to be managed intensively. Periodic regional estimates of mean colony size, in conjunction with aerial censuses, would provide the necessary information to detect temporal changes in beaver populations. Although the night-vision equipment did not perform well enough for me to confidently assign age-classes, the correlation that I found between the number of beaver observed in these censuses and the actual number present in the colony suggests that periodic nocturnal counts of random colonies is a useful method of monitoring changes in the mean size of beaver colonies.

Removal trapping was expensive and time-consuming, but on my research areas, it was the only method that provided accurate information on colony composition and reproductive rates. Clark and Andrews (1982) recommend that colony estimates be updated every 2 years to reflect changes in colony composition. Surveys of the same colony have shown a 34% fluctuation in colony size in subsequent years (Swenson et al. 1983). Periodic complete trapping of a random sample of colonies appears to be the best method of monitoring trends in the composition and demographics of beaver colonies in Illinois.
LITERATURE CITED


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<th>Age-class</th>
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<th>Percent with fetuses</th>
<th>Fetuses per breeding female</th>
<th>Daughters born per female (m.)¹</th>
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¹ Calculated as the proportion of females breeding times the number of fetuses/female x 0.5 female offspring. The proportion of females that breed in each age-class was based on the percentage of females in the next older class with corpora albicantia. Because trapping was conducted during the breeding season, the percentage of females with corpora lutea or with fetuses would underestimate the actual percentage that breed.
Table 2. Life table for beavers (*Castor canadensis*) based on the known age at death of 148 beavers harvested from trapped out colonies in central and southern Illinois. The number of kits at birth was estimated from the age of breeding females in each colony and age-specific fetal rates.

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Table 3. Fecundity table of beavers (*Castor canadensis*) from lightly exploited colonies in central and southern Illinois.

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<td>0.02</td>
</tr>
<tr>
<td>13.5</td>
<td>0.01</td>
<td>1.62</td>
<td>0.02</td>
</tr>
<tr>
<td>14.5</td>
<td>0.01</td>
<td>1.62</td>
<td>0.02</td>
</tr>
</tbody>
</table>
Table 4. Whole body weights and skinned weights (kg) of beavers (*Castor canadensis*) collected in central and southern Illinois, January-March 2000 and 2001.

| Age-class | N  | Whole Body Weight | | Skinned Body Weight |
|-----------|----|--------------------|-------------------|
|           |    | Mean Weight | SD | Range | N | Mean Weight | SD | Range |
| 0.5       | 59 | 8.9        | 1.6 | 3.2 - 11.4 | 72 | 6.8        | 1.3 | 2.7 - 9.8 |
| 1.5       | 45 | 13.5       | 2.4 | 10.0 - 19.1 | 56 | 10.4       | 1.7 | 7.3 - 14.6 |
| 2.5       | 33 | 17.7       | 1.7 | 15.0 - 23.6 | 39 | 13.3       | 1.7 | 10.7 - 18.6 |
| ≥3.5      | 57 | 22.3       | 3.3 | 15.5 - 32.2 | 60 | 16.9       | 2.5 | 12.6 - 23.2 |
Table 5. Mean colony size of beavers (*Castor canadensis*) reported in previous studies.

<table>
<thead>
<tr>
<th>State/Province</th>
<th>Mean no. beaver/colony</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>New Brunswick</td>
<td>3.2</td>
<td>Nordstrom 1972</td>
</tr>
<tr>
<td>Saskatchewan</td>
<td>3.5</td>
<td>Gunson 1970</td>
</tr>
<tr>
<td>Alaska</td>
<td>4.1</td>
<td>Boyce 1974</td>
</tr>
<tr>
<td>Montana</td>
<td>4.1</td>
<td>Easter-Pilcher 1990</td>
</tr>
<tr>
<td>Newfoundland</td>
<td>4.2</td>
<td>Bergerund and Miller 1977</td>
</tr>
<tr>
<td>Michigan</td>
<td>5.1</td>
<td>Bradt 1938</td>
</tr>
<tr>
<td>West Virginia</td>
<td>5.3</td>
<td>Swank 1949</td>
</tr>
<tr>
<td>South Carolina</td>
<td>5.5</td>
<td>Woodward 1977</td>
</tr>
<tr>
<td>Illinois</td>
<td>5.6</td>
<td>this study</td>
</tr>
<tr>
<td>Ohio</td>
<td>5.9</td>
<td>Svendsen 1980</td>
</tr>
<tr>
<td>Massachusetts</td>
<td>6.2</td>
<td>Hodgdon 1978</td>
</tr>
<tr>
<td>Massachusetts</td>
<td>8.1</td>
<td>Brooks et al. 1980</td>
</tr>
<tr>
<td>Nevada</td>
<td>8.2</td>
<td>Busher et al. 1983</td>
</tr>
</tbody>
</table>
Table 6. Comparison of the age classes present in each of the harvested samples of beavers (*Castor canadensis*).

<table>
<thead>
<tr>
<th>Age</th>
<th>Total Sample (N=239)</th>
<th>Trapped Sample (N=169)</th>
<th>Solicited Sample (N=70)</th>
<th>Typical Age-ratios (from Hill 1982)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kits</td>
<td>32.2%</td>
<td>32.5%</td>
<td>31.5%</td>
<td>30.1%</td>
</tr>
<tr>
<td>1.5</td>
<td>23.9%</td>
<td>21.9%</td>
<td>28.6%</td>
<td>22.8%</td>
</tr>
<tr>
<td>2.5</td>
<td>17.6%</td>
<td>12.4%</td>
<td>30.0%</td>
<td>≥2.5 = 47.1%</td>
</tr>
<tr>
<td>3.5</td>
<td>7.9%</td>
<td>10.1%</td>
<td>2.9%</td>
<td>--</td>
</tr>
<tr>
<td>4.5+</td>
<td>18.4%</td>
<td>23.1%</td>
<td>7.2%</td>
<td>--</td>
</tr>
</tbody>
</table>
Table 7. Average litter sizes of beaver (*Castor canadensis*) from various areas in North America.

<table>
<thead>
<tr>
<th>State/Province</th>
<th>Mean # Embryos</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>California</td>
<td>2.3</td>
<td>Busher (1987)</td>
</tr>
<tr>
<td>Alabama</td>
<td>2.5</td>
<td>Wilkinson (1962)</td>
</tr>
<tr>
<td>Mississippi</td>
<td>2.6</td>
<td>Wigley et al. (1983)</td>
</tr>
<tr>
<td>Wyoming</td>
<td>2.9</td>
<td>Osborn (1953)</td>
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<tr>
<td>Alaska</td>
<td>3.1</td>
<td>Boyce (1981)</td>
</tr>
<tr>
<td>Maine</td>
<td>3.6</td>
<td>Provost (1958)</td>
</tr>
<tr>
<td>Michigan</td>
<td>3.7</td>
<td>Bradt (1939)</td>
</tr>
<tr>
<td>Ohio</td>
<td>3.8</td>
<td>Henry and Bookhout (1969)</td>
</tr>
<tr>
<td>Wisconsin</td>
<td>3.9</td>
<td>Peterson and Payne (1986)</td>
</tr>
<tr>
<td>Illinois</td>
<td>4.0</td>
<td>this study</td>
</tr>
<tr>
<td>South Dakota</td>
<td>4.0</td>
<td>Dieter (1992)</td>
</tr>
<tr>
<td>Pennsylvania</td>
<td>5.5</td>
<td>Brenner (1964)</td>
</tr>
</tbody>
</table>
Fig. 1. Age composition of 239 beavers harvested in central and southern Illinois, January-March, 2000 and 2001.
Fig. 2. Percentage of beavers in each age-class from completely harvested research colonies versus those harvested by cooperating trappers. Cooperators rarely trapped all of the beavers from any colony.
Fig. 3. Relationship between body weights of beaver kits and the date that they were trapped.
Winter Weight Change in Yearling Beavers

Fig. 4. Relationship between body weights of yearling beavers and the date that they were trapped.

r= -0.17; N=44; P=0.267
Fig. 5. Relationship between body weights of adult beavers and the date that they were trapped.
Fig. 6. Mean sex-age composition of 28 beaver colonies in central and southern Illinois.
Fig. 7. Relationship between the number of beavers present in a colony and the maximum number of beavers observed during nocturnal censuses using night-vision binoculars.