

SEX AND AGE COMPOSITION OF SPRING-HUNTED EURASIAN BEAVER IN NORWAY

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Abstract: In Norway, Sweden and Finland most Eurasian beaver (*Castor fiber*) harvested are shot in April and May. As beaver cannot be sexed or effectively aged under spring hunting conditions, hunters normally shoot the first animal seen. The consequences for population management are so far unknown. We tested the hypothesis that 1) the age composition and reproductive status of beaver shot did not

vary significantly as individuals were removed sequentially from colonies and 2) the sex ratio of shot beaver did not deviate significantly from a 50:50 distribution. We investigated the sex, age and reproductive status of 126 beaver shot with rifles between 13 March and 15 May, 1997-99, on a 242 km² land area in southeast Norway. The sex ratio of fetuses and all age groups did not deviate significantly from 50:50. The age ratio of the pooled bag was 14% juveniles, 22% 2-year-olds and 63% adults. Adults and pregnant females were more likely to be shot first from colonies than others, the later probably because the increased nutritional demands of late pregnancy exposed them more to hunters. Removal of an estimated 22-26% of the beaver population each year, of which 25% was pregnant females, was seemingly the main cause of the decline in occupied colonies from 57 to 31 (46%) during 3 years. The apparent susceptibility of adults and pregnant females to spring shooting should be considered when designing management plans for beaver.

Key words: age composition, beaver, *Castor canadensis*, *Castor fiber*, hunting, Nordic Countries, Norway, populations, population control, sex composition

The management of hunted populations of wildlife often involves selective harvest by sex and age to achieve specific management goals. Not all harvested species, however, show sufficient sex or age-specific morphological differences to enable hunters to shoot selectively. In such instances, individuals may either be shot in proportion to their occurrence within the population, or some form of selection for specific sex and age groups may occur. Ideally, the sex and age structure of the harvest and any inherent biases should be known, as harvest mortality can influence

the population's subsequent growth rate and sex and age composition (Strickland et al. 1994).

Throughout most of North America beaver (*Castor canadensis*) are traditionally harvested by trapping from late autumn to early spring (Novak 1987). Some studies have suggested a bias in trapped samples towards adults (Novakowski 1965:40, Boyce 1974:35) while others suggest no bias (Novak 1977, Payne 1982). Dieter (1992) found a predominance of males in the 4.5 + age-class among spring-shot beaver in South Dakota. This study, however, involved the shooting of primarily nuisance animals under peak flood conditions during a special season extension, and therefore cannot be considered a study of normal harvest conditions.

In Europe and Asia, the Eurasian beaver is presently being harvested almost exclusively by trapping throughout the former Soviet Union and in Estland, Latvia and Lithuania. In continental Europe, beaver populations are presently expanding (Nolet and Rosell 1998), though open seasons for hunting and trapping have yet to be initiated. However, in the Nordic countries of Finland, Sweden (Hartman 1999) and Norway (Parker and Rosell 2001), hunting beaver with firearms during spring has been the dominating harvest form for the past 3-4 decades. As both Eurasian and North American beaver cannot be sexed from external characteristics (Wilsson 1971, Novak 1987), and are difficult to age under hunting conditions in spring, selective harvesting by sex and age is seemingly impossible (Parker and Rosell 2001). Consequently, hunters normally shoot the first animal that provides them with a good shot. Despite expanding populations (Hartman 1994, Härkönen 1999) and the increasing popularity of spring beaver hunting in the Nordic countries, no studies have yet addressed the

question of hunter selectivity for sex and age and the potential consequences for population development and management.

In this study we investigated the sex and age composition and reproductive status of beaver shot by hunters during spring in southeast Norway. If hunters harvest sex and age groups in the same proportion as their occurrence in the population then the composition of samples of first, second and subsequent individuals shot in colonies should not vary significantly. We tested the hypothesis that 1) the age composition and reproductive status of beaver shot did not vary significantly as individuals were removed sequentially from colonies and 2) the sex ratio of shot beaver did not deviate significantly from a 50:50 distribution.

METHODS

Study Area

The study was conducted in Bø Township (59°25'N, 09°03'E; 266 km²), Telemark County, southeast Norway during 1996-99. The mountainous terrain is interspersed with small streams and lakes and is 77% boreal forest, 9% cultivated, 9% above tree line, 3% urban and 2% water. Following local extirpation in the nineteenth century, beaver first became reestablished in the township about 1920 (Olstad 1937) and appear to have reached peak density around 1970. Trapping and hunting were reopened in 1971 and until 1986 only nuisance animals were taken. From 1986-95 the harvest was light, increasing from 5 to 39 animals annually (Parker 2000). Natural predation is minimal as wolves (*Canis lupus*), the only known major predator on beaver (Novak 1987, Andersone 1999), were not resident locally. Mean density of occupied colonies for all area below tree line (242 km²) was 0.26/km² in 1995, which is typical for boreal forest in Scandinavia (Hartman 1994, Härkönen 1999).

Population Survey and Beaver Hunt

Between 16 October and 15 December, 1996-1999, all beaver habitat in Bø Township was covered on foot or by canoe. All lodges with food caches were defined as occupied (Bergerud and Miller 1977). Newly built or repaired lodges at sites where caches were not found, but where considerable tree felling and/or dam-building activity occurred were also defined as occupied, because winter caches are not always present or visible at active sites (Semyonoff 1951, Hill 1982). The number of occupied colonies in spring (March-May) was assumed to be the same as the number present the previous autumn. Rosell and Parker (1995:55) reviewed the literature on colony size in Eurasian beaver and calculated a mean colony size of 3.8 (SD = 1.0, range = 1-7, n = 13 studies). Steifetten and Uren (1997:18) conducted repeated twilight counts of beaver in 19 colonies in Bø Township in August/September, 1995, and obtained a mean colony size of 3.8 (SD = 1.8, range = 1-7). As this was considered a minimum value, and because 4.0 is a commonly used multiplication factor for estimating the autumn population size of Eurasian beaver in the Nordic countries (Rosell and Parker 1995:56), we multiplied the number of occupied lodges by 4 to obtain an estimate of the autumn population size. Our goal was to shoot 25% of the estimated autumn population each year, primarily during the spring hunt. This harvest goal was initially selected as it lay slightly below the limit for sustained yield management for beaver occupying boreal forest of average quality at northerly latitudes (Payne 1984a, Novak 1987).

Beaver show a crepuscular-nocturnal active period and a diurnal inactive period (Buech 1995) and most hunting therefore occurs near dawn and dusk. Hunters were instructed to hunt in a normal fashion by shooting the first beaver that offered a good shot. To reduce the loss of carcasses from sinking, hunters were also asked to shoot

only animals that were standing in shallow water or on land. With the exception of one beaver shot from a canoe, all animals were shot by hunters from shore.

Beaver were shot with center-fire rifles between 13 March and 15 May, 1997-99. Twenty different hunters bagged at least one animal. In southeast Norway beaver can be hunted and trapped from 1 October to 30 April. In Bø Township, however, we were allowed an extension to 15 May for the duration of the study to ensure that the goal of a 25% harvest could be achieved. Permission to hunt beaver beyond the normal open season was granted by the Norwegian Directorate for Nature Management and the affected landowners.

The sex and age composition of the population prior to initiation of the spring hunt was unknown. Animals were weighed to the nearest 0.1 kg, autopsied, and sexed by internal inspection of sex organs. They were aged from patterns of tooth irruption and root closure, or from counts of cementum annuli (van Nostrand and Stephenson 1964), and categorized as juveniles (young born the previous year), 2-year-olds (i.e. just short of 24 months) or adults. Pregnant females were defined as those containing at least one living fetus when shot. Fetuses were sexed from the presence or absence of testicles.

Beaver defend territories (Aleksiuk 1968, Rosell et al. 1998) and colonies may consist of a reproducing pair plus young from 1 or 2 litters, single individuals of either sex, or various congregations of mixed sex and age groups, but normally with only 1 sexually mature female present (Wilson 1971, Novak 1977, Lancia and Hodgdon 1983). We assumed statistical independence between colonies, i.e. the removal of one or more individuals from one colony had no effect on the behavior or composition of individuals in other colonies within the short time span animals were harvested during the spring

hunt (13 March – 15 May). Each beaver shot was assigned to a specific colony based on our knowledge of autumn colony location and, for some streams, the location of territorial borders (Rosell et al. 1998).

We used chi-square analysis to test the hypotheses that 1) the age and reproductive status of second individuals shot in colonies did not differ significantly from that of first individuals shot and 2) there were no deviations from a 50:50 distribution in the sex ratio of different age groups. The level for statistical significance was set at $p \leq 0.05$.

RESULTS

We shot 143 beaver during the 3 years including 134 (94%) between 13 March and 15 May (hereafter spring-shot beaver) (Table 1). The remaining were shot or trapped as nuisance animals between 1 October and 12 March. One hundred twenty-six of the spring-shot beaver were autopsied (Table 1) of which 64 (51%) were shot during the last 2 weeks of the normal spring hunting season and 34 (27%) during the post-season extension of 1-15 May. Ninety-two percent were shot during evening and the remainder during early morning. Beaver were harvested from a mean of 51% of the occupied colonies and a mean of 1.9 animals were removed per harvested colony during the 3 years. The mean harvest rate of the estimated autumn population was 24% (Table 1).

The age ratio of the pooled bag was 14, 22 and 64% for juveniles, 2-year-olds and adults, respectively (Table 2). The proportion of juveniles in the bag declined from 26% to 3% during the 3 years, while the proportion of 2-year-olds and adults increased slightly. There was no significant deviation from a 50:50 sex distribution for any age

class (Table 2). The sex ratio for 70 fetuses from 28 pregnant females was 39 males and 31 females and did not deviate significantly ($p = 0.339$) from 50:50.

The ratio of juveniles, 2-year-olds and adults in the bag varied significantly ($p < 0.001$) between the samples of first and second individuals shot in colonies for all years pooled (Table 3). The adult proportion declined from 76 to 50%, while that of juveniles and 2-year-olds increased. Likewise, the proportion of pregnant females, adult males and others (juveniles, 2-year-olds and non-pregnant adult females pooled) varied significantly ($p = 0.015$) between the samples of first and second individuals shot in colonies for all years pooled. The proportion of pregnant females declined from 31 to 14%, the proportion of adult males showed little change, while the group of remaining individuals, primarily juveniles and 2-year-olds, increased from 32 to 53%. The pregnant female was shot in 43% of the colonies harvested from and in 22% of the colonies present in the township. The number of occupied colonies in autumn declined from 57 to 31 (46 %) during the 4 years (Table 1).

DISCUSSION

Previous studies of the selectivity of trapping (Bradt 1947, Henry and Bookhout 1969, Boyce 1974) and hunting (Dieter 1992) on beaver sex and age ratios have been difficult to interpret as the initial composition of the populations in question has been poorly known, and indeed difficult to obtain. Though the present study is no exception, our analysis of individuals shot sequentially in colonies indicates that adults and pregnant females were more prone to being shot first than other colony members. The greatest selection for pregnant females and adults will presumably occur when colonies are harvested by shooting one individual from many colonies, as opposed to many animals from few colonies. This may be particularly true when primarily family

colonies are harvested, as single and pair colonies tend to contain a high proportion of adults (Boyce 1974, Payne 1980, 1982). Thus selectivity depends upon the proportion of individual colonies harvested, the proportion of the total population harvested and colony composition, as well as the trapping or hunting methods utilized (Bradt 1947, Novakowski 1965:40, Parker and Rosell 2001, Parker et al. 2001). The degree of selectivity will gradually diminish as the proportion of the population harvested increases (Novak 1977), regardless of the method used.

The pre-hunt proportion of pregnant females in the population was unknown. However, assuming one pregnant female per colony (Wilson 1971, Novak 1977, Lancia and Hodgdon 1983) and a mean colony size of 4 (Rosell and Parker 1995:55) we estimated the pre-hunt pregnant female proportion of the population to be 25%. Not all beaver colonies, however, contain breeding females (Payne 1982), and most likely our population was no exception. Thus this percentage could be lower. Therefore our finding that 31% of the first individuals shot were pregnant females also provides strong evidence of hunter selection for this group.

The greater susceptibility of pregnant females to being the first shot in colonies may be related to the nutritional demands of late pregnancy. The energy requirements and food intake of pregnant mammalian females are from 17 to 32% higher than for non-reproducing females (Robbins 1993:200). Beaver are active under ice for up to 7 months, relying mainly on the bark of stored woody vegetation, and adults often lose weight at this time (Novakowski 1967). Following spring breakup, animals are no longer confined by ice and fresh food again becomes available. Buech (1995) found that breeding adult female beaver used 52% of their active time period in May and June for feeding, compared to 29% for adult males. Parker et al. (2001) found that pregnant

females were shot further from the lodge than other beaver. This suggests that pregnant females are more active in their search for presumably more and better quality food during spring than other colony members, apparently exposing themselves more to hunters.

The predominance of adults in the sample of first individuals shot may also be coupled to adult male scent-marking behavior. Beaver scent-mark most frequently in spring (Rosell et al. 1998) and adult males apparently more frequently than other family members (Aleksiuk 1968, Buech 1995). As most beaver in this study were shot on land, this may have increased the susceptibility of adult males to being shot.

Most beaver were shot on land, a common hunting practice in Norway. If adults, and males in particular, scent mark more frequently than other age groups then beaver shot in the water may have a different sex and age composition than those shot on land. Likewise, beaver shot at southerly latitudes where water does not freeze and scent-marking is infrequent (Novak 1987) may show other patterns of selection. Our results are consistent with other research showing that most Eurasian beaver are shot during the last 2 weeks of the spring season in late April or early May (Hartman 1999, Parker and Rosell 2001).

Despite no prior knowledge of the age class composition of the populations in question, a comparison of beaver age class ratios between studies may suggest trends in the selectivity of hunting compared to trapping. Novak (1987) in Table 8 summarized beaver age class ratios obtained from trapped populations in various areas of North America. We combined this data (minus Benson 1936, Gunson 1967 and Payne 1975) with data from Leege and Williams (1967) and Welch et al. (1993) to obtain a mean \pm SD and (range), respectively, for 23 studies of $33\% \pm 11$ (16-66) for juveniles, $23\% \pm 8$

(10-43) for 2-year-olds and $44\% \pm 14$ (8-66) for adults. Dieter's (1992) study of spring-shot North American beaver ($n = 159$) revealed respective values of 20, 23 and 58%, i.e. similar to our values of 14, 22 and 64%. Though numerous factors including e.g. habitat quality (Gunson 1970:36, Semyonoff 1951) and harvest history (Boyce 1981, Payne 1982) may influence the age distribution of populations, the relatively high proportion of adults and low proportion of juveniles in Dieter's (1992) study and ours suggests that spring shooting may be more selective of adults, and less of juveniles, than late fall-to-spring trapping.

We found no significant deviation from the 50:50 sex ratio for all age classes pooled, for 70 fetuses, or for individual age classes, though males tended ($p = 0.059$) to dominate among 2-year-olds. Likewise, Dieter (1992) found no significant deviation in the sex ratio of spring shot beaver, though males tended to dominate among adults > 4.5 years old. In contrast, Novak (1987) reviewed the literature and found that for primarily trapped populations, the sex ratio heavily favored males in the juvenile and 2-year-old classes and females among adults.

The model we employed aimed at harvesting 25% of the autumn population, a level we initially believed sustainable. The 46% decline in the autumn population of occupied colonies over 3 years however, suggests that considerable over-harvesting occurred during our harvest period. Sustainable yield harvest is dependant upon the proportion of the population harvested, as well as the sex and age ratio of individuals taken. Hunter inability to avoid shooting adult females resulted in 25.4% of the harvest as pregnant individuals. Additionally, many of the same colonies were harvested from in consecutive years, allowing little opportunity for reproduction to occur in these. The combined effect of harvesting from 46-59% of the active colonies each year, a

minimum mean takeoff of 43% of the pregnant adults from these, and an estimated mean annual harvest of 24% was apparently the main reason for the declining proportion of young in the bag and the eventual fall in number of active colonies. Population productivity may be particularly sensitive to the removal of females in late pregnancy. If this occurs during or shortly after the normal breeding period in late January and February, subdominant and sexually suppressed 2-year-olds or adults could come into heat following the removal of the dominant adult female living in the same colony (Payne 1984b). However, pregnant females removed as late as April and May would unlikely be compensated for.

There is also evidence that our goal of a 25% harvest was exceeded during the second and third years, as average colony size may decline in response to the removal of productive females (Payne 1975). We assumed a mean colony size of 4.0 when calculating autumn population size each year. In reality, colony size may have declined as production fell, resulting in an estimated population size greater than the actual. Evidence for this can be seen in the decline in the mean and maximum number of beaver shot per harvested colony from 2.2 to 1.7, and from 6 to 4, respectively, during the 3 years.

As our study was not a controlled field experiment, other factors could have caused the rapid fall in number of active autumn colonies we observed, in the absence of spring hunting (Busher and Lyons 1999). Such factors include disease (Addison et al. 1987), exceptionally cold winters (Boyce 1974), spring flooding (Kennelly and Lyons 1983) or deteriorating food conditions (Aleksiuk 1970). However, as we have no evidence for alternative explanations, we tentatively conclude that over-harvesting was the main cause.

Management implications

When management goals involve population control, and hunting is the main harvest form, spring shooting will tend to reduce the reproductive output of populations by selecting for adults and pregnant females. This will be particularly true if the harvest is spread among many colonies (Parker et al. 2001). This exploitation may lead to an earlier mean age at sexual maturity for females (Boyce 1981) and a smaller mean litter size (Payne 1975). Alternatively, where high productivity is desired, concentrating the hunting effort to as few colonies as possible should result in a reduced takeoff of adults and pregnant females, particularly when family colonies are those primarily harvested. Additionally, hunting nearer the lodge and attempting to shoot smaller individuals may reduce the take off of pregnant females (Parker et al. 2001). Some hunters and non-hunters alike may react negatively to the felling of females in the advanced stages of gestation, with resulting consequences for the public acceptance of late spring beaver hunting (Parker and Rosell 2001). Maximum sustained yield for Eurasian beaver in the Nordic countries most likely lies between 10-20% when spring hunting is the major harvest form, depending mainly upon habitat quality (Gunson 1970:59, Novak 1987) and how colonies are harvested (Parker et al. 2001). This is lower than most values suggested for trapped populations of both species (Novak 1987).

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Table 1. The number of occupied colonies, estimated population size and harvest of Eurasian beaver in Bø Township, southeast Norway, 1996-99.

	1996	1997	1998	1999	Pooled ($\bar{x} \pm SD$)
Number of occupied colonies in autumn and following spring	57	52	39	31	
Estimated autumn population (occupied colonies x 4)	228	208	156		592
Nuisance beaver trapped/shot 1 October – 12 March		3	3	3	9
Number shot 13 March – 15 May that sank (no autopsy)		4	2	2	8
Number shot 13 March – 15 May and autopsied		50	41	35	126
(% of estimated autumn population)		(22%)	(20%)	(22%)	(21 ± 1%)
Total harvest		57	46	40	143
(% of estimated autumn population)		(25%)	(22%)	(26%)	(24 ± 2%)

Number of colonies harvested from, autumn to spring	26	25	23	74
(% of occupied colonies)	(46%)	(48%)	(59%)	(51 ± 7%)
Number of pregnant beaver shot	14	11	7	32
(% of colonies harvested from)				(43%)
Mean number of beaver shot/colony	2.2	1.8	1.7	(1.9 ± 0.3)
(range)	(1-6)	(1-5)	(1-4)	

Table 2. Age distribution of Eurasian beaver shot between 13 March and 15 May in Bø Township, southeast Norway, 1997-99.

	1997	1998	1999	Pooled	Male	Female	p ^a
	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)	<i>n</i> (%)			
Juveniles	13 (26)	4 (10)	1 (3)	18 (14)	8	10	0.637
2-year-olds	7 (14)	14 (34)	7 (20)	28 (22)	19	9	0.059
Adults	30 (60)	23 (56)	27 (77)	80 (64)	40	40	1.000
Sum	50 (100)	41 (100)	35 (100)	126 (100)	67	59	0.476

^aThe probability of deviation from a 50:50 sex distribution.

Table 3. The proportion of juvenile, 2-year-old and adult Eurasian beaver and the proportion of pregnant females, adult males and others (juveniles, 2-year-olds and non-pregnant adult females pooled) in the samples of first and second individuals shot in colonies between 13 March and 15 May in Bø Township, southeast Norway, 1997-99.

	<u>Sequence shot in colony</u>		p
	First <i>n</i> (%)	Second <i>n</i> (%)	
Juveniles	6 (9)	6 (17)	
2-year-olds	10 (15)	12 (33)	
Adults	52 (76)	18 (50)	
Sum	68 (100)	36 (100)	<0.001
Pregnant ^a	21 (31)	5 (14)	
Adult males	25 (37)	12 (33)	
Others	22 (32)	19 (53)	
Sum	68 (100)	36 (100)	0.015

^a22 adults and four 2-year-olds