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Authors: Parker, Howard, and Rosell, Frank


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Rapid rebound in colony number of an over-hunted population of Eurasian beaver *Castor fiber*

**Howard Parker and Frank Rosell**

*H. Parker (howard.parker@hit.no) and F. Rosell, Faculty of Arts and Sciences, Dept of Environmental and Health Studies, Telemark Univ. College, NO-3800 Bø i Telemark, Norway*

The current reestablishment and growth of beaver *Castor fiber* populations throughout Eurasia has created a need for methods to control population size. While lethal-trapping has been the most common harvest and control method for beaver world-wide for centuries, in recent decades spring hunting has developed as the main lethal method in Norway, Sweden and Finland. An experimental hunt where hunters annually removed 22–26% (mean = 24%) of the estimated spring population of beavers on 242 km$^2$ in southeast Norway led to an unanticipated 46% decline in colony number after only three years. We monitored the population response in colony number throughout the ensuing four years of no hunting during which time the number of colonies rebounded by 93%. The rapid increase in colony number suggested a high rate of dispersal to vacated colony sites by animals from unexploited colonies within the study area (approximately half were unexploited each year) and from bordering townships where harvest was light at the time. Increased fecundity usually follows in the wake of a significant reduction in the density of mammal populations and most likely contributed to the rapid rebound in colony number observed. We conclude that spring hunting can be employed to significantly reduce population size when desired and that over-exploited populations may rebound quickly after hunting stops when dispersing individuals are in adequate supply from colonies both within and outside the harvested area.

Following its near extirpation in the latter half of the 19th century, the Eurasian beaver *Castor fiber* has since become reestablished throughout much of its former range (Halley et al. 2012). Though still legally protected in most European Union (EU) countries, member states may implement measures to control individuals and populations when necessary, including the use of lethal methods (Pillai and Heptinstall 2013). Beaver can presently be hunted and/or trapped as a game species throughout much of Eurasia including EU member states Sweden, Finland, Latvia, Lithuania and Estonia, in non-member Norway and in many countries of the former Soviet Union (Parker et al. 2002). It is likely that some form of population exploitation or control will eventually be necessary in most other Eurasian countries where beaver populations become reestablished (Parker and Rosell 2003). An ongoing example is the German state of Bavaria. Here nuisance beaver for many years were live-trapped and translocated to sites both within and outside Germany. Now that the local carrying capacity has been reached and the demand for surplus beavers for European stocking and reintroduction has mostly ended, the live-trapping and euthanasia of hundreds of animals annually has become a common practical solution (Pillai and Heptinstall 2013).

While still an important harvest form for furbearers world-wide, lethal trapping as a method to manage populations has gradually been losing public support (Gentile 1987, Batcheller et al. 2000). Simultaneously, populations of many native and alien furbearers requiring some form of control have been on the increase. These concurrent though opposing trends have motivated an interest in new methods to utilize and control expanding populations of beaver and other furbearers (Batcheller et al. 2000, Iossa et al. 2007). In Fennoscandia (Norway, Sweden and Finland), use of the leg-hold trap became illegal during the early 20th century in the wake of the near extirpation of the beaver in this region (Hartman 1999, Parker and Rosell 2003). As beaver populations recovered and interest in trapping waned, hunting with firearms gradually became the dominant harvest form for beaver here. This trend has continued to the present (Parker and Rosell 2001).

In response to the dearth of information on how hunting affects beaver populations, Parker et al. (2002) investigated the sex and age composition and reproductive status of beaver shot by hunters during spring in southeast Norway, when most beaver in Fennoscandia are hunted (Parker and Rosell 2001). Their goal (Parker et al. 2002) was to shoot 25% of the population each year during three consecutive years on 242 km$^2$ (colony density = 0.26 km$^{-2}$), primarily during spring. They estimated the spring population size, i.e. number of individual beaver, by multiplying the number of colonies found during the previous autumn by 4, this being the mean colony size commonly employed for Eurasian beaver based on previous studies (Parker et al. 2002). They employed this mean value for colony size since a precise count...
of the number of individual beaver in many colonies using non-lethal methods is both difficult and laborious (Rosell et al. 2006). A 25% harvest level they believed would not notably reduce colony number or mean colony size as it lay slightly below the limit for sustained yield of 30% reported for winter-trapped North American beaver Castor canadensis occupying similar habitat in Ontario, Canada (Novak 1987) and for winter-trapped Eurasian beaver in the former Soviet Union under best conditions (Dezhkin and Safonov 1966). Although their harvest goal of 25% was achieved (actual three-year mean harvest rate was 24%, range = 22–26%), the number of colonies in autumn (n = 57) unexpectedly declined by 46% during the three-year study (Parker et al. 2002). From their bag composition analysis they concluded that the unexpected decline in colony number was mainly a result of adults, and pregnant females in particular, being more susceptible to spring shooting than two-year-olds and juveniles, a trend seldom observed in trapped populations (Parker et al. 2002). Likewise, parturition date was delayed the following year in colonies where the adult male had been shot the previous spring, which in turn may have led to lower survival of late-born young and therefore lower recruitment (Parker et al. 2007).

Here we 1) present the response in colony number during the four ensuing years immediately following the three-year experimental hunt when no hunting occurred and 2) attempt to explain this response in light of the apparent causes of the decline in colony number reported by Parker et al. (2002).

**Methods**

The study was conducted in Bø Township (59°25'N, 09°03'E), Telemark County, southeast Norway during 2000–2003. With the exception of a few nuisance animals removed, no hunting occurred during these ensuing four years following the three-year experimental hunt. Between 16 October and 15 December of 2001 and 2003 all beaver habitat (242 km²) in Bø Township was covered on foot or by canoe using the same method employed during the preceding experimental hunt (Parker et al. 2002). All lodges or bank dens with either new autumn food caches (Bergerud and Miller 1977) or where considerable tree-felling or dam-building activity occurred (Semyonoff 1951, Hill 1982) were defined as occupied by a colony of one or more beavers.

**Results**

After four years of no hunting the number of colonies in autumn had rebounded from 31 to 53, or to 93% of the pre-experimental hunt level of 57 colonies (Fig. 1).

**Discussion**

Since the experimental hunt was not a controlled field experiment, a similar decline in colony number on the study area could have occurred in the absence of spring hunting (Bushar and Lyons 1999). However, potential contributing causes of mortality including disease (Addison et al. 1987), exceptionally cold winters (Boyce 1974), spring flooding (Kennelly and Lyons 1983) and deteriorating food conditions (Aleksiuk 1970) were not experienced on either the study area or in neighboring townships. Therefore Parker et al. (2002) concluded that over-harvesting was the main cause of the decline in colony number observed. Likewise, though a detailed study was not conducted, there was no indication that a similar, simultaneous and independent rapid increase in colony number occurred post-hunt in townships bordering the study area. This suggests that the observed, rapid post-hunt increase in colony number on the study area was primarily a response to the decline that occurred during the experimental hunt.

The pause in hunting during the ensuing four post-hunt years enabled colony number to increase unhindered by harvesting. To what degree the increase in colony number reflected the actual increase in beaver number, however, is unknown. The rapid increase in colony number suggests some dispersal to vacated colony sites by animals from bordering regions where harvest was light at the time (Parker and Rosell 2012). However, we suspect most dispersing individuals originated from neighboring unexploited colonies within the study area, which annually constituted 46–59% of those colonies present each year during the three-year hunt (Parker et al. 2002). Many dispersing and re-colonizing individuals were probably sexually mature two- or three-year-olds (Boyce 1981, Hartman 1997) and therefore able to breed during their first year of colonization. Increased fecundity usually follows in the wake of a significant reduction in the density of mammal populations (Sinclair et al. 2006) and most likely contributed to the rapid rebound in colony number observed.

In the initial study (Parker et al. 2002), hunters were instructed to hunt in the normal fashion, i.e. to shoot those beavers that offered a good shot, stopping the hunt when the total quota was reached. Since not all colonies are
equally accessible or easy to hunt on, beaver were eventually shot from only about half of the colonies each year. As such, the harvest results tend to reflect the normal beaver hunting situation in Norway, which was an initial goal of the study. Had hunters been instructed to shoot the first individual that offered a good shot from each colony, but no others, the proportion of pregnant females in the bag would likely have been considerably higher, since pregnant females are more susceptible than others to being the first shot from colonies (Parker et al. 2002). A higher take-off of pregnant females would most likely have led to a slower rebound in the number of colonies than that actually observed.

**Management implications**

Spring hunting may assist in achieving a reduction in colony number when desired, where lethal trapping of beaver is not allowed. Whereas live-trapping and euthanasia usually entail an expense (Pillai and Heptinstall 2013), hunters normally pay to hunt beaver, or do it at no expense. In instances where a beaver population has been considerably reduced from over-exploitation, where dispersing individuals are in adequate supply, and where sufficient dispersal routes are present, populations may be expected to rebound quickly when hunting is suspended.

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