EVALUATION OF INDUCED STERILITY FOR BEAVER *(CASTOR CANADENSIS)* MANAGEMENT PROBLEMS [1]

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The concept of controlling animal damage problems by reducing fecundity of offending species through induced sterility first was proposed by Knipling (1955) for insect control and was applied successfully by that author (Knipling 1959) for eradication of the screwworm fly. The potential application to vertebrate pest problems was recognized immediately by David (1961) and, subsequently, by many other workers for a variety of pests (e.g. Balser 1964; Kennelly et al. 1970; Murton et al. 1972; McDonald 1980; Potvin et al. 1982) including beaver (Arner 1964; Blanchard 1964; Nevers 1968; Hill 1977). Unfortunately, the method remains today largely unavailable for routine application to vertebrate pests.

Two primary reasons that reproductive inhibition has not progressed much beyond the experimental stage are the failure of previous studies to investigate this approach critically for specific vertebrate problems and the use of inappropriate experimental designs when testing efficacy of chemosterilants. The latter problems resulted in confounding reproductive effects and unexpected behavioral changes. Applicability of the concept to animal damage problems invariably has been assumed rather than determined by research. Quite possibly, expected benefits will not occur because unrecognized individual and population behavioral mechanisms may exist that allow targeted species to compensate, thereby raising the cost-benefit ratio to unacceptable levels.

Several studies have illustrated the need to address this question. Murton et al. (1972) considered reproductive inhibition for control of feral rock doves *(Columba livia)* until it was found that two-thirds of the population were non-breeders. They concluded that administration of a chemosterilant to the entire population would be too costly for the likely benefits; mass baiting would have created additional problems. Rodent control studies provide another example. Numerous studies to develop a male chemosterilant were undertaken before it was shown that potential benefits were probably much lower than had been assumed (Kennelly et al. 1972). Although 85% of an adult male population of Norway rats *(Rattus norvegicus)* was sterilized, fecundity was unaffected, because adult females were sufficiently promiscuous to offset the treatment. Similarly, the well-known polygynous breeding behavior of red-winged blackbirds *(Agelaius phoeniceus)* has been the rationale for numerous studies designed to develop a male chemosterilant; the assumption being that one sterile male would reduce the fertility of all females on his territory. However, Bray et al. (1975) showed that red-winged females were more promiscuous than had been recognized previously and that fertile clutches were produced despite male sterility. Again the benefits from sterilization were below expected levels.

Here, we evaluate the feasibility or adpatability of reproductive inhibition to beaver control problems.

GENERAL CONSIDERATIONS

Beaver breeding patterns indicated the method might be successful. Unlike most mammals, beaver are considered monogamous and once paired, the bond continues for years. They breed once yearly, whether or not a litter is successfully reared. Reproductive life extends up to and, in some cases, well beyond a decade. These 3 facts; monogamy, one annual breeding cycle, and long reproductive life suggested that the benefits to be expected from sterlizing a breeding adult should be cost effective. An important study objective was would beaver alter their breeding behavior when 1 adult was sterile, i.e., would the pair-bond be broken and colony integrity lost? Also, monogamy has been inferred from numerous observations but any involvement of sexually mature subadult male colony members in the presence of the adult male had never been assessed. The potential existed for mating to occur between the adult female and sexually mature offspring, a situation that could completely offset expected effects of adult male sterilization.

A literature review suggests that beaver damage in suburban or rural areas would be ameliorated if fecundity could be suppressed in a cost-effective manner. When pelt prices are high, trapping is an economical means of control and reproductive inhibition is unnecessary. However, the reverse is frequently true and without financial incentives to trap, control is left largely to state and federal agencies, a generally more costly alternative. An important factor is the fact that the damage is fre-

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quently the result of young dispersing beaver moving into unoccupied areas. Parent colonies, rather than being problems themselves, often are regarded highly for the numerous benefits they produce in local ecosystems. Thus sterilization of adults in many colonies producing nuisance beaver might be very cost-effective. Besides the obvious advantage of reducing or eliminating a source of nuisance animals, the local ecosystem benefits would be prolonged because "parent" colonies would utilize the available food base at a lower rate.

A third factor of increasing importance today but often overlooked is public acceptance of reproductive inhibition as a substitute for killing. Humane societies overwhelmingly support neutering domestic pets, because they consider it the best strategy for dealing with millions of stray and feral animals that must be killed annually. Also to be considered is the fact beaver create numerous problems in areas such as State and National Parks where killing is prohibited but reproductive inhibition might be allowed.

This study was designed initially to be a 2-year effort, the first year for selecting and treating each colony and the second year for assessing colony behavior and reproduction. The results were published (Brooks et al. 1980). However, when an opportunity arose to continue treatment evaluation for an additional 2 years, the project continued without interruption and is the basis of this report (Lyons 1979). In the interest of providing the reader with the most complete narrative possible for critically evaluating the technique and our interpretation of the results, we have included some of the previously published results.

METHODS

The studies were conducted on Prescott Peninsula which is located within Quabbin Reservation, a municipal water supply for metropolitan Boston, Massachusetts. Study colonies were part of an essentially unexploited beaver population because public access to and trapping on the area were prohibited. The spatial relationships between study colonies and other colonies on the study area are illustrated in Figure 1. Brooks et al. (1980) provide more detailed information on colony selection and surgical procedures; the more pertinent details are provided here.

COLONY SELECTION

Eighteen colonies were selected using the following criteria: sufficient habitat to support colonies for several years, presence of 3 age classes (breeding adult pair and the 2 most recent litters), and presence of a yearling (0.5-1.5 years old) the same sex as the sterilized adult. Initial live-trapping, sexing, tagging (metal and colored plastic ear tags), and treatment occurred between July and October of the first year.

TREATMENT

Sterility was performed surgically for treated colonies; controls received the same surgical procedure short of sterilization. The following 4 treatment regimes were established: controls (n = 4), Colony Nos. 1, 2, 3, 4; female oviducal ligation (n = 5), Colony Nos. 5, 6, 7, 8, 9; male vasectomy (n = 5), Colony Nos. 10, 11, 12, 13, 14; and castration (n = 4), Colony Nos. 15, 16 (female castrate) and 17, 18 (male castrate).

OBSERVATIONS

All Prescott Peninsula colonies were surveyed each fall after food cache construction had begun and other signs denoting an active colony site (lodge repair, fresh scent mounds, etc.) could be expected; shore colonies were surveyed again each spring. The 18 study colonies were monitored more intensively during these biannual surveys to identify and count residents at each active site. Each spring and summer, attempts were made to retrap colonies if identification of individuals differed from expected or if they had relocated. Two types of colony moves were noted: seasonal moves in which the animals shifted activity centers to different lodges or locations in the same vicinity or territory, and major moves that were usually sudden, generally permanent and to more distant sites.

Assessment of changes in colony social structure was based primarily on observational data supplemented by live-trapping to confirm parturition, to mark previously unmarked beavers and to provide positive identification when doubt existed. For example, when colonies moved or when beaver appeared in unexpected locations, frequency of observations at the site was increased, and live-trapping was initiated. It was important, particularly with the 18 adult pairs, to accurately identify colony members.

RESULTS

POPULATION DENSITIES

Beginning in 1968, the number of active beaver colonies on Prescott Peninsula was estimated annually through ground and boat surveys. The maximum number of active colonies, 46, occurred in 1975, the year preceding the study's initiation. Colonization of new sites after 1975 usually was associated with abandonment of older sites. Total active colonies on the Peninsula during the 3 years were 44, 42, and 44, respectively (Table 1).

COLONY INTEGRITY

A summary of the persistence of pair bonds by colony years, a measure of colony integrity throughout the study, is presented in Table 2. There was no evidence of pair-bond disruption in the 4 control colonies. However, data on 2 control colonies was not available

Table 1. Number and density of active beaver colonies on study area.

Year	No. active sites[a]		Total	Density (colonies/km)	
	Stream	Shore		Stream	Shore
1976	30	14	44	0.71	0.32
1977[b]	28	14	42	0.67	0.32
1978	30	14	44	0.71	0.32
Mean	29	14	43	0.70	0.32

[a] Determined by presence of food cache, recent lodge maintenance or animal sighting.
[b] Survey incomplete; number of active sites was estimated.

for the third year because of relocation to unknown sites.

Among 10 colonies selected for tubal ligation, only 2 provided strong evidence that the pair-bond was intact at the conclusion of the study. Four colonies showed evidence of pair-bond disruption and 4 colonies relocated to unknown sites preventing assessment of pair bonds.

Evidence for pair-bond disruption occurred among 3 of 4 castrate colonies. In 1 instance, Colony 16, the castrated female left the colony within a few weeks of ovariectomy and was replaced by another adult female. The 2 colonies containing castrated males were definitely affected by treatment. In both situations the males appeared to be either rejected by colony members or departed of their own accord. At the start of the second year, both males were observed living alone in the vicinity of the colony but not associated with it and by the third year each had joined another colony. In one case, the "adopted" colony was fertile because kits were observed. Both castrated males showed considerable alopecia during the summer months of the first year, the only time this condition was observed during the study. Behavior of both males was atypical, particularly the male at colony 18.

Nondispersing 2-year-olds were observed in each colony that remained intact (original adult pair present) through the second and third year. However, only 1 of 4 intact colonies showed this pattern the first year. Since this phenomenon occurred among the control colonies, the sterilization procedures and any associated effects were probably not responsible.

COLONY REPRODUCTION

The reproductive success of all study colonies is summarized in Table 3.

Table 3. Summary of colony reproduction.

	Annual Colony Fertility					
	Treated (n = 14)			Control (n = 4)		
	Sterile	Fertile	No Data	Sterile	Fertile	No Data
1976	11	2	1	0	4	0
1977	7	2	5	0	4	0
1978	3	4	7	1	1	2
Total	21	8	13	1	9	2

Reproduction occurred in at least 9 of 12 breeding cycles represented by control colonies. In the third year, we could find no evidence that reproduction occurred in 1 control colony while 2 other controls relocated to unknown sites preventing an assessment of reproduction. With 1 colony exception that occurred the first year of the study, subadult 2-year-old beavers remained in control colonies 1 or more years longer than expected (Novakowski 1965; Wilsson 1971).

Reproduction did not occur in at least 14 of 30 breeding cycles in colonies containing either a vasectomized adult male (n = 5) or a tubal-ligated adult female (n = 5). The remaining 16 cycles were either fertile (4 cycles) or reproduction could not be determined (12 cycles) because colonies had relocated to unknown sites. The 4 fertile breeding cycles occurred in 2 male-ligate colonies. In both instances, the ligated male either died or dispersed, but the adult female and other colony members remained at the site.

Three of 4 castrate colonies did not reproduce the first year; the fourth was a colony in which the treated female was replaced shortly after treatment. The aberrant behavior already noted in the 2 male castrate colonies at the beginning of the second year and their

Table 2. Summary of pair bond persistence by colony years.[a]

Treatments	Number of Stream-colony Years				Number of Shore-colony Years			
	Total	Pair Bond Status			Total	Pair Bond Status		
		Intact	Disrupted	Unknown		Intact	Disrupted	Unknown
Ligate–								
Male	9	5	2	2	6	1	3	2
Female	3	2	0	1	12	5	2	5
Castrate	6	4	2	0	6	1	5	0
Subtotal	18	11	4	3	24	7	10	7
Control	6	6	0	0	6	4	0	2
TOTAL	24	17	4	3	30	11	10	9

[a] Colony year = presence of one family group at a particular site during 1 year.

apparent exclusion from the colony did not immediately result in new pair-bond formation. No litters were observed at these sites the following spring. However, 1 adult female that paired initially with a castrate male produced kits the third year, confirming disruption of the pair-bond.

DISCUSSION

The reproductive inhibition achieved suggests that sterilization could be an effective management option for beaver in some situations. The question of whether the benefits to be expected from beaver sterilization (i.e., continual maintenance of colony integrity without reproduction each year) are realistic was answered affirmatively; 3 sterilized colonies responded exactly this way for at least 3 consecutive years. The total extent of reproductive inhibition, 21 confirmed barren breeding cycles out of a possible 42 (50%) is further evidence that sterilization has sufficient potential to justify further development as a control procedure. The fact that an equal proportion of the breeding cycles in this study were known to be either fertile (20%) or could not be evaluated because colonies had relocated to unknown sites (30%) should not be dismissed. It is quite possible that many of the latter colonies were also sterile. However, we believe factors besides treatments were responsible for reducing the effectiveness of sterilization to the 50 percent observed, factors that can be circumvented if not actually eliminated in the future. Most of the 21 breeding cycles that were either fertile or in doubt were more likely due to density-dependent factors or colony site location (i.e. shore colonies vs those on streams) or both.

TREATMENT EFFECTS

Two types of treatment effects need to be distinguished; procedural effects, those related to or caused by our procedures, and sterility effects. Procedural effects refer to all factors that can influence the reproductive outcome of treated colonies, not just the surgical procedure. While both types of treatment effects can result in significant alterations in individual or group behavior, the undesirable aspects of a procedural effect usually can be avoided by appropriate adjustments whereas behavioral changes due to being sterile, depending on frequency, would be incompatible with development of a reproductive control program.

There was evidence that procedural treatment effects accounted for some of the undesirable results, but the extent sterility affected the outcome, if at all, is less clear. The latter, unfortunately, is confounded by other factors. A total of 8 fertile cycles occurred within 4 treated colonies during the study; 7 were considered due to procedural effects of the treatment while only 1 possibly was due to sterility effects.

Treatment procedures affected 3 colonies; 2 were castrates (16, 18), and 1 was a male-ligate (13). As noted earlier, the castrated female in colony 16 abruptly disappeared after surgery and, according to behavioral observations, was replaced by a 2-year-old offspring. When the latter was trapped in spring 1976 and examined by laparotomy she was pregnant. However, this female also disappeared about a month after laparotomy and was replaced by an immigrating adult female that remained for the balance of the study. Thus, reproduction at this colony occurred each of the 3 years but involved 2 different females. Although we lack direct evidence to explain the sudden disappearance of 2 adult females in successive years from the same colony, the fact each underwent surgery several weeks earlier suggests complications associated with surgery as the probable cause. Sterility was not considered a factor for 2 reasons. First, 1 of the 2 females that disappeared was not sterilized and second, the other female-castrate colony, Colony 15, was still intact at the end of the study.

A fourth fertile cycle occurred in colony 18, a male-castrate, and was considered to be a direct result of castration on behavior with subsequent disruption of the adult pair bond. We considered this a procedural rather than a sterility effect. The method of inducing sterility, castration, is well-known to affect androgen-dependent male behavior patterns and sterilization by other means should eliminate such undesirable secondary effects. It should be noted that the other male-castrate (17) reacted similarly; colony members abandoned the area and the treated male remained alone at a new but nearby location.

The remaining 3 fertile cycles attributed to a procedural treatment effect occured at colony 13, a male-ligate colony of unusual composition. It contained several extra adult-sized animals, a fact that unfortunately was not discovered until the second year. The treated male never was identified positively upon return to the colony following surgery and probably either dispersed or died. Retrapping this colony in spring 1976 provided evidence that the adult pair, at least the female if not both, were incorrectly identified at the start of the study. In view of the treated male's disappearance and the probable misidentification of beaver, it is not surprising that reproduction occurred all three years. Nevertheless, colony 13 remained classified as a male-ligate throughout the study.

The eighth fertile cycle among treated colonies occurred the third year in colony 12, a male-ligate that had undergone major compositional changes the previous year. The treated male dispersed during the first spring (1976), was retrapped in July about 2.5 stream km away and never again was observed. The adult female remained in the vicinity until fall 1977 with no evidence that she produced young either of the first 2 years. She then relocated to an unknown site for the third winter but returned the following spring with 6 other beavers including 3 kits. Apparently she paired with another male and bred over the winter suggesting this colony might be an example of an effect on breeding behavior due to sterility *per se*.

POPULATION DENSITY

Before this study was terminated it became obvious that the Prescott Peninsula beaver population had reached maximum carrying capacity about 1975. The mean colony densities observed, 0.32 colonies/km of shoreline and 0.70 colonies/km of interior stream (Table 1), were probably maxima for the local topography and available habitat. Other workers have reported similar density values for beaver populations considered saturated (Novakowski 1965; Nordstrom 1972). Also, the number of active colonies on the Peninsula had been increasing annually throughout the decade preceding 1975, yet during this study, 1975-78, no increase occurred (Table 1). When new sites were colonized, marginal habitat or sites already abandoned by beaver were selected. Other indications of high beaver densities, increase in colony age structure (Nordstrom 1972), increased aggression (Kudryashov 1975) reduced fecundity (Novakowski 1965; Payne 1975; Bergerud and Miller 1977), were noted.

Beaver colonies usually consist of a breeding adult pair and their offspring from the 2 most recent breeding seasons; subadults generally disperse their second spring (Novak 1972, 1977). We frequently found subadults remaining an additional year or 2. For example, in 1977, 22 non-dispersing subadults were observed in 12 study colonies classified as intact, i.e. the original adult pair still present. Assuming a mean litter size of 3 kits, these colonies produced 36 potential dispersers yet 22 or 60 percent of them unexpectedly remained in the parent colony. Because this phenomena occurred in treated and control colonies alike, it was not considered to be a treatment effect. Besides, during the years when this population was expanding, subadult dispersal was 97 percent Hodgdon (1978). Further, those beaver that did disperse invariably left the area, because only 2 of 20 dispersers were retrapped on the Prescott Peninsula. There was no evidence subadults ever participated in reproduction while the adult pair was present, despite remaining an extra year or 2 in the parent colony.

We found evidence of an increased incidence of antagonistic behavior. Five of 64 beaver trapped during the second and third year had wounds suggestive of intraspecific fighting. In previous years, wounded beaver were seldom encountered in the Prescott population (Hodgdon 1978; Brooks and Lancia, personal communications). Kudryashov (1975) found that European beaver (*Castor fiber*) may be mortally wounded by conspecifics and reported that scars and fighting were more common in high density areas.

The third density-dependent indicator, reduced fecundity, was associated with 2 study colonies and was not considered a treatment effect. In 1 instance, a male-ligate colony, the adult female paired with an untreated male, produced kits the second year but not the third year. The other case involved a control colony that was barren the third year.

COLONY SITE

Major moves were made almost exclusively by shore colonies. Eight of 10 shore colonies relocated but only 2 of 8 on interior streams did so. A fluctuating reservoir level was the single most significant factor provoking relocation; differences in water level by as much as 3 meters occurred between years. This resulted at least in partial flooding of all shore colony lodges some time during this study. Three shore colonies managed to accommodate to rising water levels by either moving to a nearby inland stream (Figure 1, colony 5), by increasing lodge height (colony 6) or by the use of auxillary bank lodges in the immediate vicinity (colony 13). A fourth family (colony 16) that abandoned a shoreline site was relocated, but the other 6 never were found after making a major move. These 6 included 4 treated

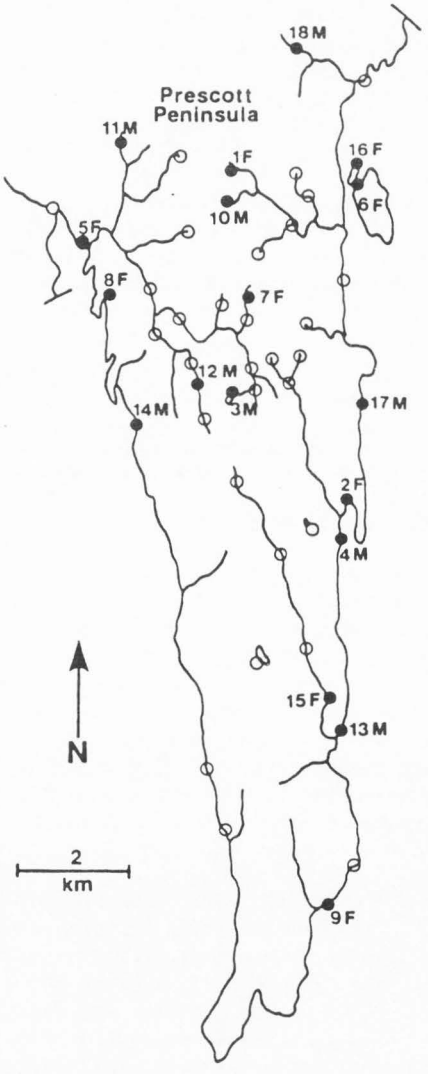

Figure 1. Active beaver colonies on Prescott Peninsula, Quabbin Reservoir, Massachusetts, in 1975. Study colonies = ●; other colonies = O; female treated = F; male treated = M.

colonies (8, 9, 14 and 17) representing all 3 treatment groups as well as 2 control colonies (2, and 4). The 4 treated colonies accounted for 8 of 13 breeding cycles for which reproductive results were unavailable. Most significant is the relocation of the 2 controls that had colonized shore sites, because it suggests that a fluctuating reservoir level rather than sterilization was the primary stimulus to relocate. Henry (1967) reported a similar effect of changing water levels on colony movement.

Further comment is needed with regard to the 2 relocated interior colonies. In 1 instance, colony 18, a male-castrate, the stimulus to move probably was related to the fact the dam and much of the lodge were washed out by a spring freshet. The male remained in the vicinity but other family members were not seen again. The second "interior" colony (5) was originally located on the Peninsula shore and, following flooding of the lodge by a rising reservoir the first spring, moved to a nearby interior stream. In spring of the second year, before reproduction by this colony could be assessed, the colony moved again and never was relocated. The fact the site was reoccupied immediately by a nonstudy family leaves unanswered why this colony abandoned an apparently suitable location.

Interior colonies 7 and 11 accounted for the remaining 3 breeding cycles for which reproductive data was unavailable. Both sites were occupied throughout the study, but, except for the treated female being identified at colony 7 the second year, we could not confirm either by observation or trapping that the original adults were present at either site the second and third year. We did confirm, however, that some of the observed beaver those years were not original members of the colony suggesting some disruption in colony integrity. Whether this was due to density dependent factors or sterilization or both cannot be resolved.

RECOMMENDATIONS

Based on the 50 percent reduction in fecundity, we concluded that nuisance beaver populations are vulnerable to reproductive manipulation and we recommend development as a control procedure. If we are but partially correct in our interpretation of why the other 50 percent of the reproductive cycles were either fertile or in doubt, our conclusion is strengthened proportionately. When planning future work we should not ignore the potential influence of sterility, population density, fluctuating water level and other factors on expected results.

We are not advocating the use of surgically induced sterility for large-scale beaver control programs; it would be an impractical solution for many damage problems. It was used primarily because of advantages if offered to the experimental design over alternative techniques. However, the value of surgical sterilization is not limited to experimental studies. The method should receive serious consideration whenever the potential benefits justify the cost or where trapping and killing is prohibited by law. It also has some application in beaver transplant operations when the purpose is to exploit this species ability to build dams and generally modify habitat; release of sterile animals eliminates any possibility that the introduced population will increase to nuisance proportions.

When selecting the means of inducing sterility, whether chemical or surgical, it is important to avoid procedures that might affect behavior. Clearly, the method of choice should not be castration, since colony behavior is affected. If surgery is deemed impractical but reproductive inhibition is still the preferred solution, research must be initiated to 1) find an effective chemosterilant and 2) develop a practical delivery system. Anything less would have a low probability for success.

We recommend that application of reproductive control procedures to high or maximum density beaver populations be carefully considered if not avoided until more becomes known about interactions between individuals within and among colonies. One alternative when confronted with such a situation is to reduce population size through killing, translocation, or both, before initiating the sterilization procedures. We also believe it would be ill-advised to select colonies for reproductive control that are located where water levels fluctuate widely during the year. It is worth noting that our observation of Prescott beaver moving between and among families may possibly be more common than previously reported; this was the first study in which a large number of individuals were identified and monitored for several years. Both in theory and practice, discrete family units with minimal intercolony movement is a major prerequisite for an effective reproductive control program. Thus, situations such as high beaver density or shoreline colony sites that might in themselves cause or promote disruption of colony integrity are best avoided when selecting colonies for reproductive control.

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