

Surgical Sterilization: An Underutilized Procedure for Evaluating the Merits of Induced Sterility

By James J. Kennelly and Kathryn A. Converse

Abstract: Despite more than 4 decades of effort, development of effective wildlife damage control programs based on sterilization of target species has met with limited success. This is partly due to the fact that investigators have assumed, rather than empirically tested, whether the reproductive strategies of the target populations were vulnerable to the planned treatment. Equally important, methods selected to induce sterility usually involve a chemical agent that can affect sociosexual behaviors of the nuisance population. In this report, we illustrate how surgically induced sterility circumvents both problems—how it enables one to assess the feasibility and applicability of the concept without the potentially confounding secondary effects of a chemical. We assessed the merits of initiating

research to develop a male chemosterilant for Norway rats, red-winged blackbirds, beaver, and Canada geese by inducing sterility surgically. The infidelity of many red-winged females to their polygynous territorial male was surprising and argued against searching for a male sterilant. On the other hand, beaver and Canada goose studies confirmed previous reports that both form pair-bonds and are monogamous. Both should be vulnerable to a male chemosterilant approach, and research toward this goal is justified.

Keywords: vertebrate pest, beaver, rodent, Canada goose, blackbird, surgical sterilization

Introduction

The concept of alleviating animal damage problems by reducing nuisance populations to acceptable numbers using induced sexual sterility has been researched for more than 40 years. Initially proposed for control of the screw-worm fly *Callitroga hominivorax*, the concept's validity was demonstrated by the eradication of this species from the island of Curaçao (Bushland and Hopkins 1951, Knipling 1955). The potential benefits of the concept compared to alternative pest control methods were recognized immediately (Knipling 1959).

Most attempts to induce sterility of vertebrate pest species have relied on use of a chemosterilant or antifertility agent. The most notable of these is the work of Elder (1964) and Wofford and Elder (1967), which resulted in the development and marketing of Ornitol® (20,25-diazocholesterol dihydrochloride), an antifertility agent for feral pigeon control.

Success of induced sterility programs has been somewhat less than expected due to failure to understand mating strategies and related sociosexual behavior patterns of species targeted for reproductive control. Investigators often assumed, rather than empirically assessed, the feasibility of this approach for each problem situation. The question of whether or not a particular nuisance species may be vulnerable to fertility control often can be answered readily by inducing sterility surgically.

A few studies that utilized surgical procedures deserve mention. Neville (1983) and Neville and Remfry (1984) maintained several discrete populations of feral cats at acceptable levels by capture and surgical sterilization of all healthy adults. While the initial cost of castration was high, the authors estimated the long-term expense, including periodic castration of subsequent newcomers, was about half the cost of alternative eradication programs. Bailey (1992) described successful introduction of surgically sterilized red foxes (*Vulpes vulpes*) to two Alaska islands where native avifauna were adversely impacted by Arctic foxes (*Alopex lagopus*). Because the two species were not sympatric on islands in Alaska, Bailey achieved the desired results of biological control. Nine years after introduction of sterile red foxes, Arctic foxes had disappeared and only one island had a few remaining red foxes. Another study demonstrates successful use of surgical sterilization to provide an indirect treatment effect. Five wolves (*Canis lupus*) were vasectomized before release in northern Minnesota to assess whether such males could keep mates and maintain territories (Mech and Fritts 1993). The rationale from a control perspective was that the absence of pups to feed might reduce livestock depredations. The results indicated that vasectomized wolves maintained pair bonds and territories and suggested that sterilization might be the technique of choice around farms experiencing livestock losses.

Proceeding on the premise that the polygynous mating strategy of feral horses (*Equus equus*) (i.e., dominant males maintain a harem throughout the year) would render this species particularly vulnerable to sterilization, Eagle et al. (1993) vasectomized 20 dominant males in each of 2 separate populations. Foaling was reduced for 2 years in bands containing a sterile male, and the treatment was considered efficacious. However, due possibly to movement of females between bands and breeding by subordinate or bachelor males, the reduced fecundity was insufficient to lower the population to an acceptable level.

Any discussion of advantages and disadvantages associated with utilization of surgically induced sterility depends largely on whether the procedure is intended to resolve research questions as proposed here or if it is intended to directly resolve a wildlife damage problem. Primary research advantages are permanency of the procedure, which allows long-term effects to be assessed for target species, and absence of behavioral or secondary effects that may accompany other methods of induced sterility. The advantages of irreversibility of the technique extend to situations where it is intended to be the method of choice for ameliorating a damage problem. The main disadvantages of surgical sterilization, the need to have the animal in hand and the expense of the procedure, limit its use. However, the value of surgical sterilization to answer important biological questions can often justify the time and expense. This report describes studies that illustrate use of surgical sterilization to better understand mating strategies and associated behavioral patterns and in some instances provide a definitive answer to damage problems.

Mating Strategies

The classification of the four mating systems pertinent to the topic at hand follow those reported by Wittenberger (1979). For the purpose of this report only the definitions for the general classification of each are given:

(1) Monogamy: "prolonged association and essentially exclusive mating relationship between one male and one female at a time."

(2) Polygyny: "prolonged association and essentially exclusive mating relationship between one male and two or more females at a time."

(3) Polyandry: "prolonged association and essentially exclusive mating relationship between one female and two or more males at a time."

(4) Promiscuity: "no prolonged association between the sexes and multiple matings by members of at least one sex."

Norway Rats (*Rattus norvegicus*)

The discovery of U-5897 (3-chloro-1, 2-propanediol) in the late 1960's as an effective sterilant for male laboratory rats (Ericsson 1970) stimulated interest in evaluating U-5897 as a potential reproductive inhibitor for control of free-ranging Norway rats. This interest occurred despite knowledge that Norway rats, with their promiscuous mating system, were considered to be unlikely candidates for male reproductive control (Knippling 1959, Marsh and Howard 1970). In fact, the latter authors postulated that in a polygamous mating system "relatively few non-sterile males can compete successfully for females against an overwhelming number of males." Since this premise was never tested empirically and since several other promising male chemosterilants appeared at that time, a study was initiated to address efficacy of male sterilization for Norway rats.

Kennelly et al. (1972) induced sterility in 85 percent of the adult males in one of two similar populations of Norway rats and compared fecundity and related parameters after 105 days by collecting and examining all juvenile and adult animals in each population. The results confirmed the postulate of Marsh and Howard (1970) and others (Davis 1961, Knippling and McGuire 1972) that development of a male chemosterilant for polygamous vertebrate pests offers little if any promise as a population control technique.

Although fecundity was reduced somewhat in the treated colony (table 1), the treatment appeared to be essentially ineffectual from a population perspective. This conclusion was based on the fact that the total number of pregnancies of the original adult population was almost equal and that the total progeny produced, 110 v. 130 in the treated and control group, respectively, differed by only 15 percent. The similarity in number of pregnancies between the two colonies is noteworthy. Based on necropsies at study termination, juveniles were capable of breeding by day 70 of the study. Although this is much sooner than was previously reported by Calhoun (1962), it indicates the majority of original females in the sterile colony conceived when only three original fertile males were available. Although one can justifiably argue that population density established at the outset was partially responsible for the fecundity level observed and that a larger enclosure might have reduced the number of fertile encounters, the study design did not permit this factor to be evaluated. Significant reduction ($P < 0.05$) in first litter size for the treated colony was attributed to the large number of vasectomized males. Adler and Zoloth (1970) reported inhibition of sperm transport and reduced litter size following multiple vaginal or cervical stimulations of female rats within 15 minutes of copulation.

Beaver (*Castor canadensis*)

Once virtually eliminated from much of its range in North America, the beaver has made such a remarkable recovery that it is now considered a serious nuisance species. The continual encroachment of humans into areas considered suitable beaver habitat has resulted in an ever-increasing number of beaver-human conflict situations. This circumstance, together with society's increasing reluctance to trap and kill offending animals, has generated considerable interest in developing induced sterility as a nonlethal alternative.

Nuisance beavers appear to be an ideal target for developing reproductive control procedures. Beavers breed once yearly regardless of whether the litter is successfully reared. They exhibit a long reproductive life, sometimes exceeding a decade

Table 1. Reproductive comparisons between a control and male sterility-induced colonies of Norway rats 105 days after treatment (from Kennelly et al. 1972)

Reproductive parameter	Control (100% of males fertile)	Treated (15% of males fertile)
Adult females		
No. pregnancies	38	39
Size first litter	10.8	8.6
Progeny		
Total produced	130	110
No. pregnancies	11	4

Table 2. Sterility treatments of breeding adults

Sterilization method	Number of colonies	
	Female	Male
Ligation ¹	5	5
Castration	2	2
Control (fertile) ²	2	2

¹ Female = oviduct; male = vas deferens.
² Sham operated.

(Larson 1967). They are reported to be monogamous (Seton 1928, Wilsson 1971, Boyce 1974), and once paired, they maintain the pair bond indefinitely barring death of one beaver or disruption of colony integrity by external factors. Other colony members do not breed despite the fact that they are sexually mature by 1.5 years of age. However, should one of the pair-bonded adults die or disappear, the remaining mate will generally pair-bond with one of the sexually mature progeny.

In 1980–83, two studies were conducted to determine the effect that induced sterility of the breeding adults might have on sexually mature but nonbreeding colony members. The objective was to assess whether sterilization would promote mating between the fertile adult and a sexually capable offspring and whether colony integrity would persist after all pretreatment offspring dispersed (Brooks et al. 1980, Kennelly and Lyons 1983). A total of 18 beaver colonies with at least 3 age-classes (adults, 1- to 2-year-olds, and <1-year-olds) were selected and assigned to treatments as shown in table 2.

Assessment of colony fecundity was on the basis of annual breeding cycles, i.e., whether or not reproduction occurred each year a colony was monitored. Therefore by definition, the maximum number of breeding cycles per colony was 3 and the total for all sterilized colonies was 42 (14 × 3) and control was 12 (4 × 3). There was no evidence of breeding outside the pair bond existing at the time of sterilization for all colonies remaining intact. Reproduction was successfully inhibited in 21 of 42 "sterile" colony breeding cycles (table 3). Reproduction in the remaining 21 was either undetermined because the colonies migrated to undiscovered sites (13), or external factors disrupted family associations to the extent that only some members could be relocated. It is noteworthy that castration adversely affected colony behavior, integrity, and fecundity in three (2 male, 1 female) of the four colonies treated in this manner. The fourth, a female-castrate, maintained the adult pair-bond throughout the study and did not produce any kits. We concluded that:

- The beaver monogamous mating system was reaffirmed.
- Adult × progeny breeding does not occur following induced sterility of one of the breeding pair.
- Tubal ligation does not affect colony sociosexual behavior, but castration does.
- Sterilization of either sex is equally efficacious.

Red-Winged Blackbirds (*Agelaius phoeniceus*)

The combined gregarious and granivorous behavior of red-winged blackbirds have been a continual problem for humans despite repeated attempts to reduce, if not eliminate, the damage that they cause. When the concept of chemosterilization was initially conceived, the reported polygynous mating system of red-wings (Allen 1914, Beer and Tibbitts 1950, Nero 1956) appeared to present a point of vulnerability: sterilization of a territorial male should inhibit reproduction in all females nesting therein. Although all these researchers reported incidents of promiscuity, they were considered exceptions rather than the rule. Clearly,

Table 3. Beaver colony reproduction: 3-year summary¹

Sterilization technique	No. of colonies	Potential no. of breeding cycles ²	No. fertile breeding cycles		
			Fertile	Sterile	Unknown
Male ligate	5	15	4	7	4
Female ligate	5	15	0	7	8
Male castrate	2	6	1	4	1
Female castrate	2	6	3	3	0
Subtotal	—	42	8	21	13
Control	4	12	9	1	2

¹ From Kennelly and Lyons (1983).

² Breeding cycle = one breeding season.

Table 4. Clutch fertility on territories of vasectomized red-wing males¹

Treatment	No. of territorial males	Number of clutches			Percent fertile
		Total	Fertile	Sterile	
Vasectomy	15	32	8	24	25
Control ²	17	24	24	0	100
Totals	32	56	32	24	

¹ From table 2 in Bray et al. (1975).

² Sham vasectomy.

however, the probability of ever successfully developing an effective male red-wing sterilization program would be compromised if the incidence of female promiscuity proved to be significantly more frequent than reported. Thus, we conducted several studies to evaluate whether red-wing females were promiscuous and, if so, to what extent. The results have been published (Bray et al. 1975, Roberts and Kennelly 1977 and 1980), and the findings germane to the current discussion follow.

The percentage (25 percent) of fertile clutches observed on territories of vasectomized males (table 4) appeared to be correlated with proximity to fertile-male territories; the more distant females were from fertile-male territories, the greater the number of sterile clutches (Bray et al. 1975). Female red-wing infidelity was confirmed in subsequent studies (Roberts and Kennelly 1977 and 1980). The latter two studies

showed that there was no significant difference between fertile and vasectomized males with regard to the sociosexual behavior patterns observed: promiscuity occurred while the female was off territory, and fertile clutches on territories of vasectomized males accounted for 70 percent of the total number observed (21/30). The results indicated that red-wings are considerably more promiscuous than previously concluded, and their polygynous mating system classification should be modified accordingly.

It should be noted that a subsequent behavioral study by Monnett et al. (1984) refuted the above conclusions regarding red-wing promiscuity. Monnett's team concluded that the extra-pair copulations (EPC's) implied by our studies do not regularly occur and proposed that this major disagreement on an important aspect of red-wing mating behavior be resolved by "paternity determinations using various electrophoretic techniques as advocated by Sherman (1981)." However, Gibbs et al. (1990) conducted an in-depth parentage study of red-winged blackbirds along the lines proposed by Monnett et al. (1984), utilizing DNA marker techniques. The Gibbs team concluded that extra-pair fertilizations "due to male cuckoldry are frequent in this species." In another study supporting our results, Westneat (1993) reported that 55 of 232 red-winged blackbird nestlings' offspring tested by DNA fingerprinting were sired by EPC's.

Apparently, red-wing breeding behavior is more opportunistic than previously thought, and the cost-benefit ratio of population control by means of male sterilization needs to be reassessed. The perceived potential advantages of this approach are not as promising as once believed.

Canada Geese (*Branta canadensis*)

Nonmigratory or resident populations of Canada geese have essentially defied all efforts to effectively reduce the nuisance problems that they generate. Because Canada geese are reported to be monogamous and quite territorial during the breeding and nesting season (Akesson and Raveling 1982), the possibility exists that one or both of these characteristics might render this species vulnerable to induced

sterility. To test this, we vasectomized ganders and observed them and their mates for up to three subsequent breeding seasons.

The results reaffirmed the conclusion that Canada geese are monogamous (Converse and Kennelly 1994). Of 72 vasectomized males, 33 paired with a female for either 1 year ($n=15$), 2 years ($n=13$), or 3 years ($n=5$). These 33 breeding pairs represent 56 nesting attempts, 47 of which (84 percent) were reproductively unsuccessful. Goslings were observed with the remaining nine treated pairs. Behavioral observations suggested that in seven instances adoption was the likely explanation for presence of goslings. Probable reasons for goslings with the other two pair are unknown because behavioral observations suggest adoption was unlikely and the surgical procedure allowed virtually no room for error. We could only speculate that gosling production might be due to EPC's, which are rarely reported in Canada geese (Kossack 1950, Klopman 1962).

With one exception, the maintenance of pair bonds for 2 years and the fidelity of treated pairs to a nest site from 1 year to the next imply that sociosexual behavior patterns were not noticeably altered due to sterility treatment. The exception concerned clutch incubation time: treated pairs incubated clutches for 35 to 120 days before deserting the nest. During this extended incubation period, aggressive territorial behaviors slowly subsided.

Nuisance Abatement via Vasectomy

The results of the above studies suggested that there are some special circumstances where surgically induced sterility might prove to be a cost-effective control technique for beaver and Canada geese.

Aside from the fact that beaver colonies provide excellent material for instructional, conservational, and environmental purposes, there are few urban situations where beaver provide beneficial effects (Willging and Sramek 1989). However, beaver activity in rural and semirural areas presents some nuisance opportunities where surgical sterilization may be an effective and practical approach. If a beaver colony is creating immediate damage, nothing short of complete removal

of the offending animals will alleviate the problem. Nuisance situations that arise year after year when dispersing 2-year-olds establish colonies where none previously existed in the recent past may be alleviated in the long term by surgically induced sterility. Assuming that a small number of colonies could be tolerated in an area, sterilization of one or both breeding adults in these colonies and the removal of all other colony members should offer two desirable results. First, the beneficial effects of the colony would be maintained and the life of the colony extended due to reduced utilization of the food base. Second, the annual contribution of dispersing offspring to the population at large would be eliminated (Payne 1989), and the number of new colonies becoming established each year would be reduced proportionately. The fact that at least 50 percent of sterile colonies were intact and not producing offspring 3 years after one adult was sterilized (Kennelly and Lyons 1983) suggests that this approach has some merit. Fortunately, the extent of the value of sterilization for reducing beaver problems can be readily assessed by an appropriately designed study.

Canada geese attracted annually to the same small suburban ponds capable of holding 2–5 pairs of breeding adults often attain nuisance status upon the production of goslings. Adult geese may be tolerated, but, together with their offspring, they are usually a problem. Our findings that 17 of 18 sterilized pairs maintained pair bonds ≥ 2 years and returned to the same nest site each year suggest that the benefits of sterilization may extend for several years. Research is needed, however, to determine whether nesting sterile pairs would repel the ingress of fertile pairs. If so, the managing of geese by sterilization could be substantial.

Summary

In summary, we have discussed studies which represent four widely different mammalian and avian species and their mating strategies to illustrate use of surgical sterilization as an answer to biological questions and as an experimental technique for animal damage management. With Norway rats and red-winged blackbirds, it is apparent that male sterility is not an effective approach, although much was learned about their mating strategies. However, successful control of reproduction in beaver and Canada geese provides impetus for further infertility studies. In select situations, surgical sterilization may be the most appropriate means of achieving that desired infertility.

References Cited

- Adler, N. T.; Zoloth, S. R. 1970.** Copulatory behavior can inhibit pregnancy in female rats. *Science* 168: 1480–1482.
- Akesson, T. R.; Raveling, D. G. 1982.** Behaviors associated with seasonal reproduction and long-term monogamy in Canada geese. *Condor* 84: 188–196.
- Allen, A. A. 1914.** The red-winged blackbird: a study in the ecology of a cattail marsh. *Proceedings of the Linnaeus Society New York* 24–25: 43–128.
- Bailey, E. P. 1992.** Red foxes, *Vulpes vulpes*, as biological control agents for introduced arctic foxes, *Alopex lagopus*, on Alaskan Islands. *Canadian Field-Naturalist* 106(2): 200–205.
- Beer, J. R.; Tibbitts, D. 1950.** Nesting behavior of the red-wing blackbird. *The Flicker* 22(3): 61–77.
- Boyce, M. S. 1974.** Beaver population ecology in interior Alaska. M.S. thesis. Fairbanks, AK: University of Alaska. 161 p.
- Bray, O. E.; Kennelly, J. J.; Guarino, J. L. 1975.** Fertility of eggs produced on territories of vasectomized red-winged blackbirds. *Wilson Bulletin* 87(2): 187–195.

- Brooks, R. P.; Fleming, M. W.; Kennelly, J. J. 1980.** Beaver colony response to fertility control: evaluating a concept. *Journal of Wildlife Management* 44(3): 568–575.
- Bushland, R. C.; Hopkins, D. E. 1951.** Experiments with screw-worm flies sterilized by x-rays. *Journal of Economic Entomology* 44(5): 725–731.
- Calhoun, J. B. 1962.** The ecology and sociology of the Norway rat. Publ. 1008. Washington, DC: U.S. Department of Health, Education, and Welfare; Public Health Service. 288 p.
- Converse, K. A.; Kennelly, J. J. 1994.** Evaluation of Canada goose sterilization for population control. *Wildlife Society Bulletin* 22(2): 265–269.
- Davis, D. E. 1961.** Principles for population control by gametocides. *Transactions North American Wildlife Conference* 26: 160–167.
- Eagle, T. C.; Asa, C. S.; Garrott, R. A.; Plotka, E. D.; Siniff, D. B.; Tester, J. R. 1993.** Efficacy of dominant male sterilization to reduce reproduction in feral horses. *Wildlife Society Bulletin* 21(2): 116–121.
- Elder, W. H. 1964.** Chemical inhibitors of ovulation in the pigeon. *Journal of Wildlife Management* 28(3): 556–575.
- Ericsson, R. J. 1970.** Male antifertility compounds: U-5897 as a rat chemosterilant. *Journal of Reproduction and Fertility* 22: 213–222.
- Gibbs, J. L.; Weatherhead, P. J.; Boag, P. T.; White, B. N.; Tabak, L. M.; Hoysak, D. J. 1990.** Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science* 250: 1394–1397.
- Kennelly, J. J.; Lyons, P. J. 1983.** Evaluation of induced sterility for beaver (*Castor canadensis*) management problems. In: Decker, D. J., ed. Proceedings of the first eastern wildlife damage control conference; 27–30 September 1983; Ithaca, NY. Ithaca, NY: Cornell University Cooperative Extension: 169–175.
- Kennelly, J. J.; Johns, B. E.; Garrison, M. V. 1972.** Influence of sterile males on fecundity of a rat colony. *Journal of Wildlife Management* 26(1): 161–165.
- Klopman, R. B. 1962.** Sexual behavior in the Canada goose. *Living Bird* 1: 123–129.
- Knipling, E. F. 1955.** Possibilities of insect control or eradication through the use of sexually sterile males. *Journal of Economic Entomology* 48(4): 459–462.
- Knipling, E. F. 1959.** Sterile male method of population control. *Science* 130: 902–904.
- Knipling, E. F.; McGuire, J. U. 1972.** Potential role for sterilization for suppressing rat populations. *Tech. Bull.* 1455. Washington, DC: U.S. Department of Agriculture, Agricultural Research Service. 27 p.
- Kossack, C. W. 1950.** Breeding habits of Canada geese under refuge conditions. *American Midland Naturalist* 43: 627–649.
- Larson, J. S. 1967.** Age structure and sexual maturity within a western Maryland beaver (*Castor canadensis*) population. *Journal of Mammalogy* 48(3): 408–413.
- Marsh, R. E.; Howard, W. E. 1970.** Chemosterilants as an approach to rodent control. In: Dana, R. H., ed. Proceedings of the 4th vertebrate pest conference; 3–5 March 1970; West Sacramento, CA. Davis, CA: University of California: 55–63.
- Mech, L. D.; Fritts, S. H. 1993.** Vasectomized wolves maintain territory. *Info. Bull.* 24. Washington, DC: U.S. Department of the Interior, U.S. Fish and Wildlife Service. 1 p.
- Monnett, C.; Rotterman, L. M.; Worlein, C.; Halupka, K. 1984.** Copulation patterns of red-winged blackbirds (*Agelaius phoeniceus*). *The American Naturalist* 124: 757–764.
- Nero, R. W. 1956.** A behavior study of the red-winged blackbird, I. Mating and nesting activities. *Wilson Bulletin* 68(1): 5–37.
- Neville, P. 1983.** Humane control of an urban cat colony. *International Pest Control* 25(5): 144–145, 152.
- Neville, P. F.; Remfry, J. 1984.** Effect of neutering on two groups of feral cats. *Veterinary Record* 114: 447–450.

Payne, N. F. 1989. Population dynamics and harvest response of beaver. In: Craven, S. R., ed. Proceedings of the 4th eastern wildlife damage control conference; 25–28 September 1989; Madison, WI. Madison, WI: University of Wisconsin Extension: 127–134.

Roberts, T. A.; Kennelly, J. J. 1977. Assessing promiscuity among female red-winged blackbirds in Massachusetts. In: Transactions of the northeast fish and wildlife conference; 4–6 April 1977; Boston, MA. [Place of publication and publisher unknown]: 99–105.

Roberts, T. A.; Kennelly, J. J. 1980. Variation in promiscuity among red-winged blackbirds. *Wilson Bulletin* 92(1): 110–112.

Seton, E. T. 1928. Lives of game animals, vol. 4. Boston: C. T. Crawford: 441–501.

Sherman, P. W. 1981. Electrophoresis and avian genealogical analyses. *The Auk* 98: 419–421.

Westneat, D. F. 1993. Polygyny and extrapair fertilizations in eastern red-winged blackbirds. *Behavioral Ecology* 4(1): 49–60.

Willging, B.; Sramek, R. 1989. Urban beaver damage and control in Dallas–Fort Worth, Texas. In: Bjugstad, A. J.; Uresk, D. W.; Hamre, R. H., eds. Ninth Great Plains wildlife damage control workshop proceedings; 17–20 April 1989; Fort Collins, CO. Publ. 127. Fort Collins, CO: Great Plains Agricultural Council: 77–80.

Wilsson, L. 1971. Observations and experiments on the ethology of the European beaver (*Castor fiber* L.). A study in the development of phylogenetically adapted behaviour in a highly specialized mammal. *Viltrevy* 8: 15–266.

Wittenbeger, J. F. 1979. Social behavior and communication. In: Mauler, P.; Vandenbergh, J. G., eds. Handbook of behavioral neurobiology, vol. 3. New York: Plenum Press: 271–349.

Wofford, J. E.; Elder, W. H. 1967. Field trials of the chemosterilant SC 12937, in feral pigeon control. *Journal of Wildlife Management* 31(3): 507–515.