

## BEAVER POPULATIONS AND THEIR RELATION TO WETLAND HABITAT AND BREEDING WATERFOWL IN MAINE

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**Abstract:** The influence of beaver (*Castor canadensis*) trapping on beaver and waterfowl densities and wetland habitat is not well understood, and this information is needed by managers trying to balance beaver densities and harvest and complaints of nuisance beaver with the abundance of wetlands and waterfowl. During 1988–92 in south-central Maine, we determined the density of beaver colonies and beaver harvest, wetland characteristics, and density of breeding pairs of waterfowl on a 111-km<sup>2</sup> site recently closed to beaver trapping and a similar site open to trapping. Density of beaver colonies increased from 0.15 to 0.32/km<sup>2</sup> (113%) on the untrapped site but changed little (0.19–0.20/km<sup>2</sup>) on the trapped site. The number of beaver dams maintained by beaver and the density of beaver colonies were correlated on the untrapped site ( $r = 0.99$ ,  $n = 4$ ,  $P = 0.009$ ) but not on the trapped site ( $r = -0.18$ ,  $n = 4$ ,  $P = 0.820$ ). Number of wetlands was correlated with the density of beaver colonies during 1989–92 on the untrapped site ( $r = 0.92$ ,  $n = 4$ ,  $P = 0.081$ ) but not on the trapped site ( $r = -0.13$ ,  $n = 4$ ,  $P = 0.875$ ). Total surface area of water on the untrapped site increased from 115 to 158 ha (36%); surface area of water remained stable on the trapped area. Species of waterfowl that increased on the untrapped site included Canada geese (*Branta canadensis*) (4–9/100 km<sup>2</sup>), hooded mergansers (*Lophodytes cucullatus*) (23–29/100 km<sup>2</sup>), and mallards (*Anas platyrhynchos*) (7–12/100 km<sup>2</sup>). Numbers of wetlands used by pairs of each species of waterfowl increased on the untrapped site. Overall, a  $\geq 1$ -year closure of beaver trapping is sufficient to increase the density of beaver colonies, whereas a 2–3 year closure is necessary to increase wetland habitat. More than 3–4 years may be required to begin influencing the density of waterfowl and number of wetlands used by waterfowl.

**Key Words:** *Anas platyrhynchos*, *Anas rubripes*, beaver, black duck, *Branta canadensis*, Canada geese, *Castor canadensis*, hooded merganser, *Lophodytes cucullatus*, Maine, mallard, trapping, waterfowl, wetlands

### INTRODUCTION

Beaver (*Castor canadensis* Kuhl) are a primary influence on wetland creation, hydrology, and dynamics in North America (Naiman et al. 1988, Johnston and Naiman 1990). Beaver-created or influenced wetlands are attractive to a variety of wildlife species (Beard

1953, Hodgdon and Hunt 1955, Grover and Baldassarre 1995).

Waterfowl use beaver flowages because they produce an abundance of invertebrates (Reinecke and Owen 1980, McDowell and Naiman 1986) that provide protein for breeding pairs, nesting females, and young ducklings (Reinecke 1979). Also, beaver-impounded wetlands offer interspersions of cover and wa-

ter for isolation of territorial pairs (Ringelman and Longcore 1982) as well as brood-rearing habitat (Beard 1953, Hepp and Hair 1977, Ringelman and Longcore 1982). Flooding of timber increases structural diversity of wetlands, provides protection from predators, and creates nesting sites for cavity-nesting waterfowl (Hepp and Hair 1977). Creation and abandonment of wetlands by beaver provide natural changes in water level that influence rates of decomposition and release of nutrients, which stimulate plant growth and invertebrate production (Weller 1981). The relationship between beaver and American black ducks (*Anas rubripes* Brewster) is of particular concern because black duck numbers have declined since 1955 (Spencer 1979) and loss and degradation of wetland habitat may be a possible cause of this decline (Kirby 1988).

Despite their benefits to wetland dynamics and wildlife, beaver may damage property, and recreational trapping is the most cost-effective method for control of beavers (Purdy and Decker 1985). However, trapping may suppress populations and thus limit wetland habitat for wildlife (Knudson 1962, Ermer 1984, Gibbs et al. 1991). However, the influence of beaver trapping on beaver and waterfowl densities and wetland habitat is poorly known, and this information is needed by managers.

We conducted our study on a site recently closed to beaver trapping and an site open to trapping. On both study sites, the objectives were to (1) determine yearly changes in density of beaver colonies, (2) monitor annual numbers and morphology of wetlands, (3) examine the annual change in area of lifeforms of wetland vegetation, and (4) compare these data to annual changes in the density of breeding pairs of selected waterfowl species. We used waterfowl as an indicator of the influence of beaver on wildlife, although beaver create habitat for a diversity of wildlife species.

### STUDY SITES

We chose two 111-km<sup>2</sup> study sites in south-central Maine. From 1988 to 1992, the Dixmont Site was closed to trapping (untrapped site) and the Montville Site was open to trapping (trapped site). The untrapped and trapped sites have similar topography, are 12 km apart, and the former has a history of waterfowl studies (Ringelman 1980, Ringelman and Longcore 1982, Diefenbach and Owen 1989). The untrapped site was contained primarily within a single watershed, whereas the trapped site covered portions of 3 other watersheds. Both sites had numerous wetland complexes that were created or modified by beaver.

Upland areas at both sites were dominated by mixed, coniferous, and deciduous forests. Upland de-

ciduous vegetation included birches (*Betula* spp), northern red oak (*Quercus rubra* Linnaeus), red maple (*Acer rubrum* Linnaeus), sugar maple (*A. saccharum* Marsh.), and trembling aspen (*Populus tremuloides* Michaux). Coniferous species included balsam fir (*Abies balsamea* Linnaeus), eastern hemlock (*Tsuga canadensis* Linnaeus), eastern white pine (*Pinus strobus* Linnaeus), and spruces (*Picea* spp.). Small-scale logging operations occurred on both sites, as did agricultural activity, mainly hay and corn.

The untrapped site (closed to trapping during our study) was comprised of portions of 4 townships; at least 70% of the area within the site was open to trapping each year for 10 years prior to the study. Townships are used as management units for beaver in Maine. The trapped site was closed to trapping in 1981, had a trapping season of 1–2 months between 1981 and 1984, and a 2-month season from 1985 to 1992. The untrapped site was closed to beaver trapping from March 1988 to December 1992. The trapped site remained open to trapping from 1 January to 28 February each year. Pre-closure data on beaver, wetlands, and waterfowl were available for the untrapped site for 1986 and 1987 but were not available for the trapped site, except for the density of beaver colonies in fall 1988.

### METHODS

#### Beaver

On the untrapped site, we determined the density of active beaver colonies by ground-checking wetlands for evidence of beaver during July–August 1986–87. From 1988 to 1992, we determined the number of active lodges on both study sites by (1) an annual census (1–15 November) of active beaver lodges using a fixed-wing aircraft (Payne 1981), (2) an inspection of each lodge from the ground to verify activity, and (3) live-trapping beaver (25% of the lodges in fall of 1988, 50% in 1989, and 100% from 1990 to 1992).

On the trapped site, we determined the percent of lodges trapped each year. We contacted all trappers to verify harvest, and we compared the annual harvest of beaver to the mean pelt price of beaver each year (K. D. Elowe, Maine Dep. Inland Fish. Wildl., unpubl. data). Mean pelt price was calculated from monthly (Oct–Mar) surveys of Maine furdealers.

From July–December 1989–92, we classified the condition of the main beaver dam on all wetlands. We classified dams as (1) maintained by beaver with good water-holding ability, (2) unmaintained but holding some water, and (3) unmaintained dams having little water-holding ability.

On the trapped site, 3 large (10–50 ha) lacustrine

wetlands with man-made dams composed an average of 58% (SE = 0.41) of the surface water on the study site each year. We reported the data separately for these wetlands because beaver did not influence the area of surface water on these sites. Including these wetlands in the results would have masked beaver-induced changes in area of surface water on the other wetlands.

### Wetland Habitat

From 1986 to 1992 on the untrapped site and from 1989 to 1992 on the trapped site, we determined annual changes in the numbers of wetlands, total basin area (BNAREA), total surface area of water (SWAREA), and perimeter of SWAREA using Kirby's (1976) methods as modified by Diefenbach (1988). Basin area included the area of the wetland containing <0.10 m of water with hydrophytic vegetation and represents areas previously flooded. Basin area included wetlands that were entirely flooded, partially flooded, or abandoned by beaver with no surface water. The SWAREA was the portion of the basin that was available to waterfowl and had >0.10 m of water.

Each May, we photographed wetlands with a 35mm camera (Ektachrome ASA 200) mounted in the floor of a fixed-wing aircraft. Maps of the wetlands were made from the slides. From July to September of each year, we ground-checked each wetland to verify the accuracy of BNAREA and SWAREA delineated from slides. We used a digitizing area-line meter (Tamaya Technics, Inc.) to measure areas. We obtained rainfall data for the area from the National Oceanic and Atmospheric Administration, Asheville, NC.

We grouped lifeforms of vegetation into the following 6 categories (Ringelman [1980] as modified from Cowardin *et al.* [1979]): open water (open water with no surface vegetation), floating-leaved, emergent herbaceous (HERB), ericaceous, alder (*Alnus rugosa* Spreng.) and willow (*Salix* spp), and timber. We delineated the areas of each lifeform on the basin and surface area maps using the color slides. From July to September, we ground-checked the vegetation lifeforms on all wetlands. We classified wetlands using the method developed by Cowardin *et al.* (1979) for both the morphometric parameters of the basin area and the area of the wetland covered by >0.10 m of water.

### Waterfowl

From 15 April to 11 May in 1986–87 and 1989–92 on the untrapped site and from 1989 to 1992 on the trapped site, we conducted two ground censuses of breeding pairs of selected species of waterfowl. Five observers conducted each census over 4–5 days. Cen-

suses began 1/2 hour before sunrise by observing waterfowl for 1–2 hours on larger wetlands from ground or elevated tree platforms (Ringelman 1980). Afterwards, observers visited smaller wetlands, and all counts were completed within 4 hours of sunrise.

We used 2 censuses to estimate number of pairs of waterfowl using each wetland. We also determined the change in the mean of the total number of waterfowl from the 2 counts. To quantify use of wetlands by pairs, we determined the number of wetlands used by each species on both sites.

Waterfowl hunting was open on both sites during the study. We did not determine the harvest and survival of waterfowl; however, we assumed they were similar between sites and over time.

### Data Analysis

All wetlands on both study sites were censused, not sampled, for beaver colonies, wetland characteristics, and waterfowl. We compared data on beaver, wetlands, and waterfowl between the sites for the closure period (1989–92). We also compared the density of beaver colonies during 1988 for both sites. For the untrapped site, we made pre-closure (1986–87) and post-closure (1989–92) comparisons.

Because we collected census data, we did not use statistical tests for comparing results among years. We estimated Pearson correlation coefficients ( $r$ , 2-sided test,  $P$ -value <0.10) for relationships to provide measures of the intensity of associations between 2 variables. This study was replicated in time but not area.

## RESULTS

### Beaver

The density of active beaver colonies on the untrapped site began increasing the first year (1989) following closure to trapping and continued to increase (0.15–0.32/km<sup>2</sup>, 17–36 colonies, 113%) during 1989–92 (Figure 1). Number of colonies on the trapped site changed slightly (0.19–0.20/km<sup>2</sup>, 21–22 colonies, 5%) over the same period. On the 3 large lacustrine wetlands on the trapped site, there was 1 colony in 1988, 3 in 1989, 0 in 1990, and 1 each in 1991 and 1992.

Harvest of beaver on the trapped site declined from 39 to 18 (54%) during 1989–92 (Figure 2). The percent of colonies trapped also declined (59–37%) during the study. There were positive correlations between harvest and pelt price ( $r = 0.97$ ,  $n = 4$ ,  $P = 0.028$ ) and between the proportion of colonies trapped and pelt price ( $r = 0.86$ ,  $n = 4$ ,  $P = 0.137$ ). Although the harvest of beaver and percent of colonies trapped per year declined during the study, the density of colonies did not change.

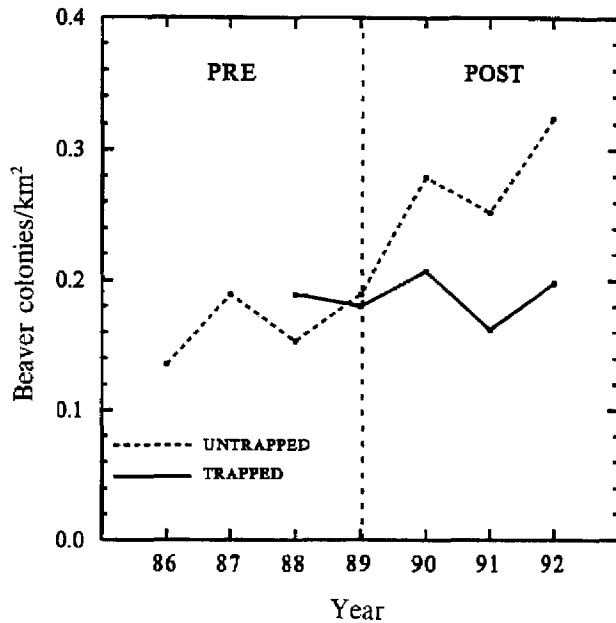


Figure 1. Beaver colonies/km<sup>2</sup> on the untrapped area during 1986–92 and on the trapped area during 1988–92, south-central Maine (PRE = before closure of trapping, POST = after closure of trapping).

The number of beaver dams maintained by beaver and the density of beaver colonies were correlated on the untrapped site ( $r = 0.99$ ,  $n = 4$ ,  $P = 0.009$ ) but not on the trapped site ( $r = -0.18$ ,  $n = 4$ ,  $P = 0.820$ ). On the untrapped site, dams maintained by beaver increased from 33 to 54 (64%) during 1989–92, those unmaintained but holding water increased from 13 to 26 (100%), and those unmaintained and not holding water declined from 27 to 13 (52%) (Table 1). On the trapped site, the number of maintained dams was stable (24–26), dams not maintained but holding water increased from 11 to 18 (64%), and unmaintained dams not holding water remained unchanged (33–32).

#### Wetland Habitat

**Numbers of Wetlands.** During 1989–92, the increase in number of wetlands was greater on the untrapped site (120 to 134) than the trapped site (103 to 110). The number of wetlands and the density of beaver colonies were correlated on the untrapped site ( $r = 0.92$ ,  $n = 4$ ,  $P = 0.081$ ) but not on the trapped site ( $r = -0.13$ ,  $n = 4$ ,  $P = 0.875$ ). Beaver created all new wetlands on both sites. Numerous wetlands were flooded and abandoned by beaver during the study, but all sites impounded by beaver in 1989 were distinguishable as wetlands in 1992; thus, no wetlands reverted to terrestrial habitat.

Precipitation for July–September ranged from 22 to 34 cm during 1986–92 (Figure 3). There was no re-

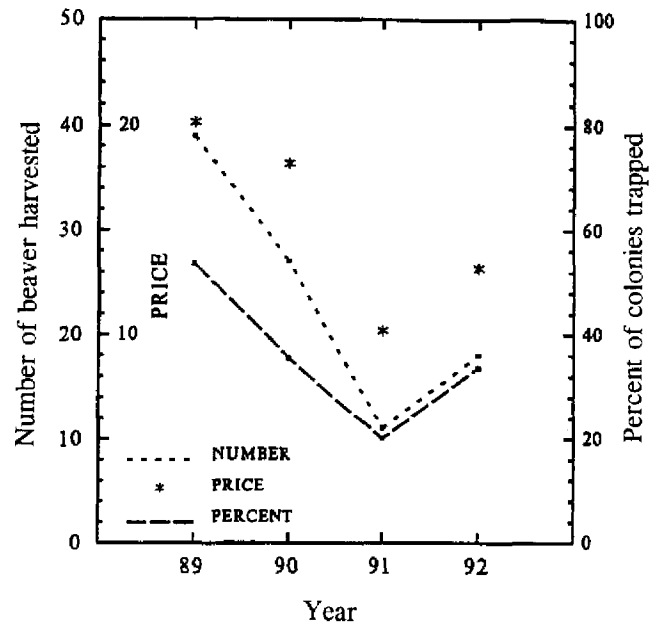


Figure 2. Number of beaver harvested and percent of colonies trapped on the trapped area in south-central Maine and mean pelt price of beaver (\$, Oct–Mar) paid by Maine fur-dealers by year, 1989–92.

lationship between precipitation (Jul–Sep) and number of wetlands on the untrapped ( $r = 0.20$ ,  $n = 4$ ,  $P = 0.802$ ) and trapped sites ( $r = 0.20$ ,  $n = 4$ ,  $P = 0.804$ ).

**Wetland Morphology.** The BNAREA increased from 456 to 475 ha (4%) on the untrapped area and from 294 to 298 (2%) on the trapped area. The percent of BNAREA flooded at the beginning of the closure period (1989) was similar between the untrapped (BNA-

Table 1. Number of beaver dams classified according to their maintenance by beaver and ability to hold water on the untrapped and trapped areas from 1989–92, south-central Maine.

Year	Dam Condition		
	Good <sup>a</sup>	Fair <sup>b</sup>	Poor <sup>c</sup>
<b>Untrapped area</b>			
1989	33	13	27
1990	46	16	18
1991	41	31	16
1992	54	26	13
<b>Trapped area</b>			
1989	24	11	33
1990	22	9	39
1991	24	10	39
1992	26	18	32

<sup>a</sup> Good = dam maintained by beaver with good water-holding ability.

<sup>b</sup> Fair = dam unmaintained but holding water.

<sup>c</sup> Poor = dam unmaintained having little water-holding ability.

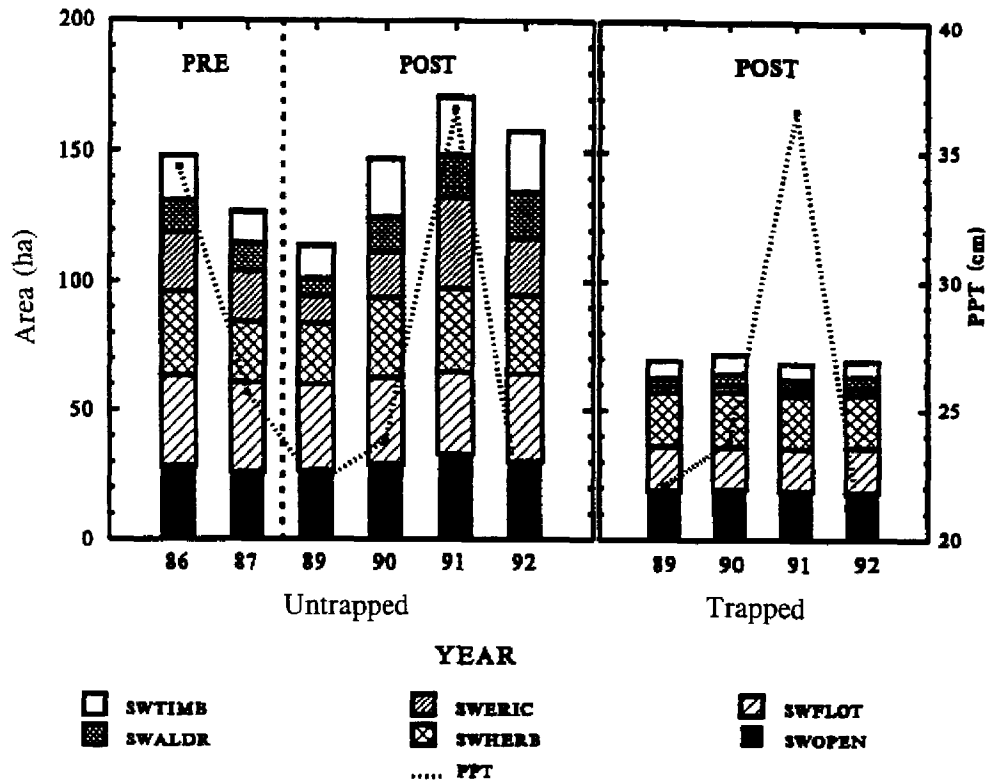


Figure 3. Total surface area of water (ha) and the portion composed of open unvegetated water (SWOPEN), floating-leaved vegetation (SWFLOT), herbaceous vegetation (SWHERB), ericaceous vegetation (SWERIC), alder and willow (SWALDR), and forested habitat (SWTIMB) on the untrapped area during 1986–92 and on the trapped area during 1989–92, south-central Maine and mean annual precipitation (PPT, Jul–Sep) 1986–92 (PRE = before closure of trapping, POST = after closure of trapping).

REA = 456 ha, SWAREA = 115 ha, 25%) and trapped sites (BNAREA = 293 ha, SWAREA = 69 ha, 23%).

During 1989–92, SWAREA on the untrapped site increased from 115 to 158 ha (36%) but declined slightly during the last year (Figure 3). On the trapped site, SWAREA remained stable. The SWAREA and the density of beaver colonies were not correlated for the untrapped ( $r = 0.67$ ,  $n = 4$ ,  $P = 0.329$ ) and trapped sites ( $r = 0.89$ ,  $n = 4$ ,  $P = 0.112$ ) but suggested positive relationships. Also, precipitation (Jul–Sep) and SWAREA were not correlated on the untrapped ( $r = 0.60$ ,  $n = 4$ ,  $P = 0.400$ ) or the trapped ( $r = -0.52$ ,  $n = 4$ ,  $P = 0.480$ ) sites. Finally, the number of wetlands and SWAREA were positively correlated on the untrapped site ( $r = 0.90$ ,  $n = 4$ ,  $P = 0.097$ ) but not on the trapped site ( $r = -0.43$ ,  $n = 4$ ,  $P = 0.568$ ).

Of the change in SWAREA on the untrapped site (1989–92), an average of 68% was caused by reflooding of existing (previously abandoned) wetlands by beaver, and 32% resulted from new impoundments created by beaver (Figure 4). From 1989 to 1992, the total perimeter of surface water increased from 85,961 to 92,442 m (8%) on the untrapped site, and from 65,693 to 67,093 m (2%) on the trapped site.

*Vegetation Lifeforms.* From 1989 to 1992, there was little change in area of each lifeform (<6 ha) within the basin on the untrapped site, except for HERB, which increased 12% (103–114 ha). On the trapped site, no lifeforms changed  $\geq 3$  ha.

The area of flooded lifeforms on the untrapped site, however, declined from 1986 to 1989 but began to increase one year following the cessation of trapping (1990) and the subsequent increase in beaver colonies (Figure 3). During 1989–92 on the untrapped site, the following flooded lifeforms increased in area: open water (27–30 ha, 12%, SWOPEN), emergent herbaceous (24–31 ha, 28%, SWHERB), ericaceous (11–22 ha, 111%, SWERIC), alder and willow (7–18 ha, 153%, SWALDR), and timber (13–23 ha, 81%, SWTIMB). Initially, SWERIC increased 235% from 1989 to 1991 because of temporary reflooding of previously abandoned wetlands, but by 1992, beaver abandoned these wetlands and SWERIC declined. On the trapped site, all flooded lifeforms changed <1 ha.

*Waterfowl*

*Density of Breeding Pairs.* The density of breeding pairs of black ducks remained relatively stable on the

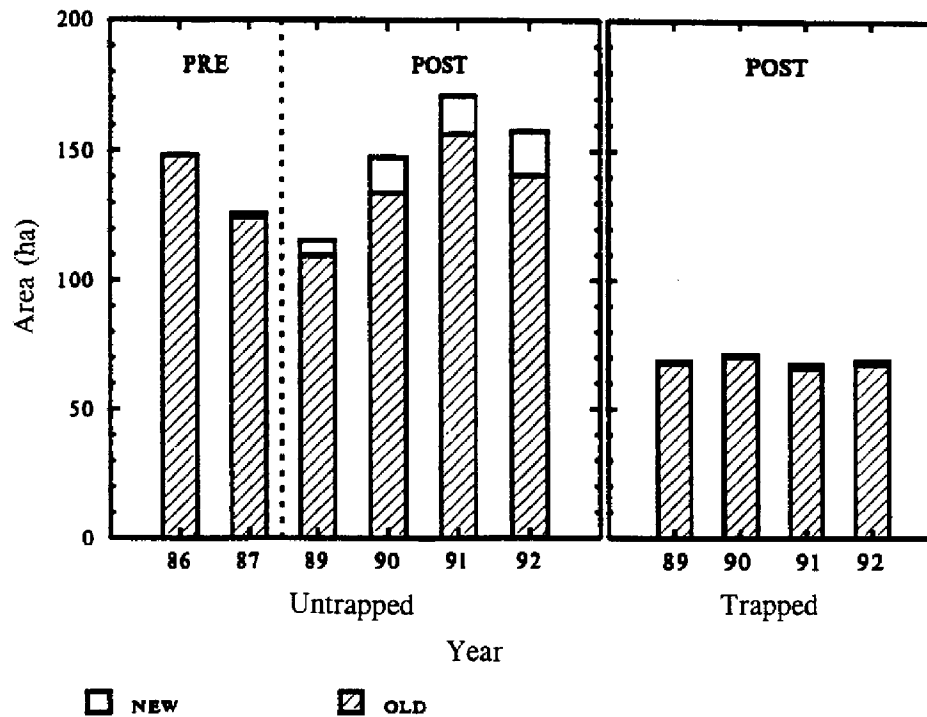


Figure 4. Total surface area of water (ha) because of reflooding of previously abandoned wetlands by beaver (old) and creation of new beaver impoundments (new) on the untrapped area during 1986–92 and on the trapped area during 1989–92, south-central Maine (PRE = before closure of trapping, POST = after closure of trapping).

untrapped (27–32 pairs/100 km<sup>2</sup>) and trapped sites (28 to 21 pairs/100 km<sup>2</sup>) from 1989 to 1992 (Figure 5). Total black ducks per 100 km<sup>2</sup> followed a similar pattern to the density of pairs on both sites. Including the number of pairs of black ducks from the 3 large lacustrine wetlands on the trapped site did not change our conclusions.

Pairs of Canada geese (*Branta canadensis* Linnaeus) increased from 4 to 9/100 km<sup>2</sup> from 1989 to 1992, and mallards (*A. platyrhynchos* Linnaeus) increased from 7 to 12/100 km<sup>2</sup>. Pairs of geese increased from 8 to 10/100 km<sup>2</sup> on the trapped site, and there was no change in the density of pairs of mallards. Many geese used abandoned beaver lodges as nest sites.

Densities of hooded mergansers (*Lophodytes cucullatus* Linnaeus) were higher on the untrapped site during the closure period (23–29 pairs/100 km<sup>2</sup>, 1989–92) than the pre-closure period (15–14 pairs/100 km<sup>2</sup>, 1986–87). The trapped site showed yearly changes of hooded mergansers similar to that of the untrapped site, and density increased from 7 to 11 pairs/100 km<sup>2</sup> from 1989 to 1992. Densities of wood ducks (*Aix sponsa* Linnaeus) were highly variable between counts within the same year; therefore, we excluded wood ducks from the analyses.

*Number of Wetlands Used by Waterfowl.* Although density of breeding black ducks changed little on the

untrapped site during the study, the number of wetlands used by pairs of black ducks increased markedly from 31 to 43 (39%) during 1989–91 then declined slightly in 1992 (Figure 6). On the trapped site, the number of wetlands used was stable (22–23) from 1989 to 1992.

The number of wetlands used on the untrapped site from 1989 to 1992 also increased for Canada geese (5–14), mallards (7–12), and hooded mergansers (16–27). On the trapped site, less change in number of wetlands used occurred for the same period: Canada geese (7–10), mallards (10–14), and hooded mergansers (5–12).

## DISCUSSION

### Beaver

On the untrapped site, beaver rapidly expanded into suitable habitat and constructed dams, which created wetlands and reflooded previously flooded wetland basins. How long this greater density of beaver colonies could be sustained remains unknown but is probably determined by the availability of the beaver's food supply of hardwoods and aquatic vegetation (Howard and Larson 1985).

In western New York, Ermer (1984) reported that a 5-year closure to beaver trapping, where the density of beaver was low relative to the available habitat, re-

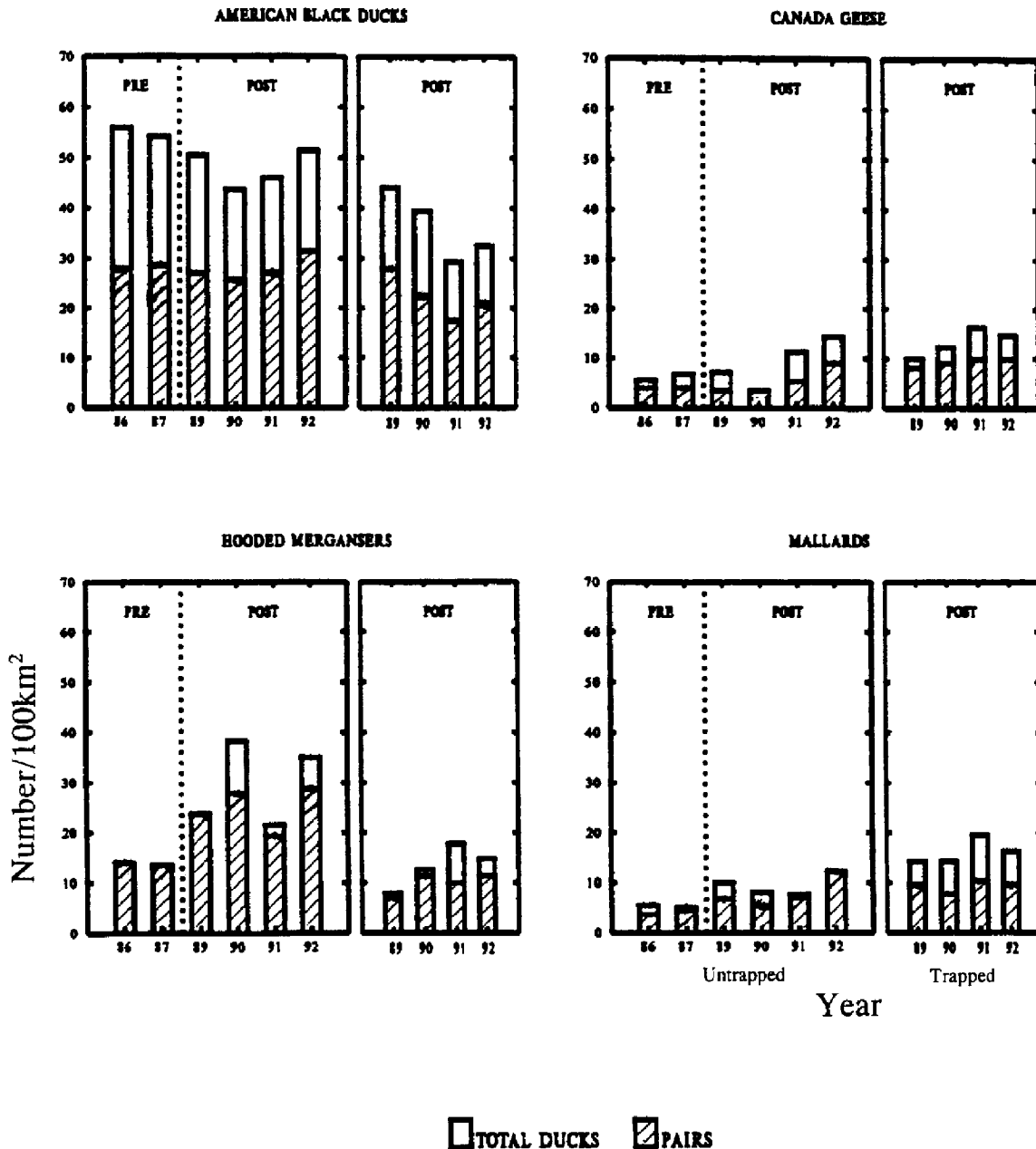


Figure 5. Density (per 100 km<sup>2</sup>) of breeding pairs and total American black ducks, Canada geese, hooded mergansers, and mallards on the untrapped area during 1986–92 and the trapped area during 1989–92, south-central Maine (PRE = before closure of trapping, POST = after closure of trapping).

sulted in an increase in active colonies of 0.03 to 0.10/km<sup>2</sup> (200%). In eastern New York, a 4-year closure resulted in an increase of 0.03 to 0.14 colonies/km<sup>2</sup> (309%) (Parsons and Brown 1978). In our study, the density of colonies at the start of the study was 5 times greater than at the beginning of the New York studies but still increased over a 4-year period. The stability in the number of beaver colonies on the trapped site (19–23), when subjected to variable trapping pressure each year (22–59% of the colonies

trapped), suggests that <20% of the colonies should be harvested per year for this site if the management objective is to increase the density of colonies and quantity and quality of habitat.

The increased number of new and refurbished beaver dams on the untrapped site can be explained by the gain in number of beaver colonies on the study site. Based on recapture of 200 tagged beaver on the 2 sites, the number of colonies increased as kits through 2-year-old beaver dispersed from their natal

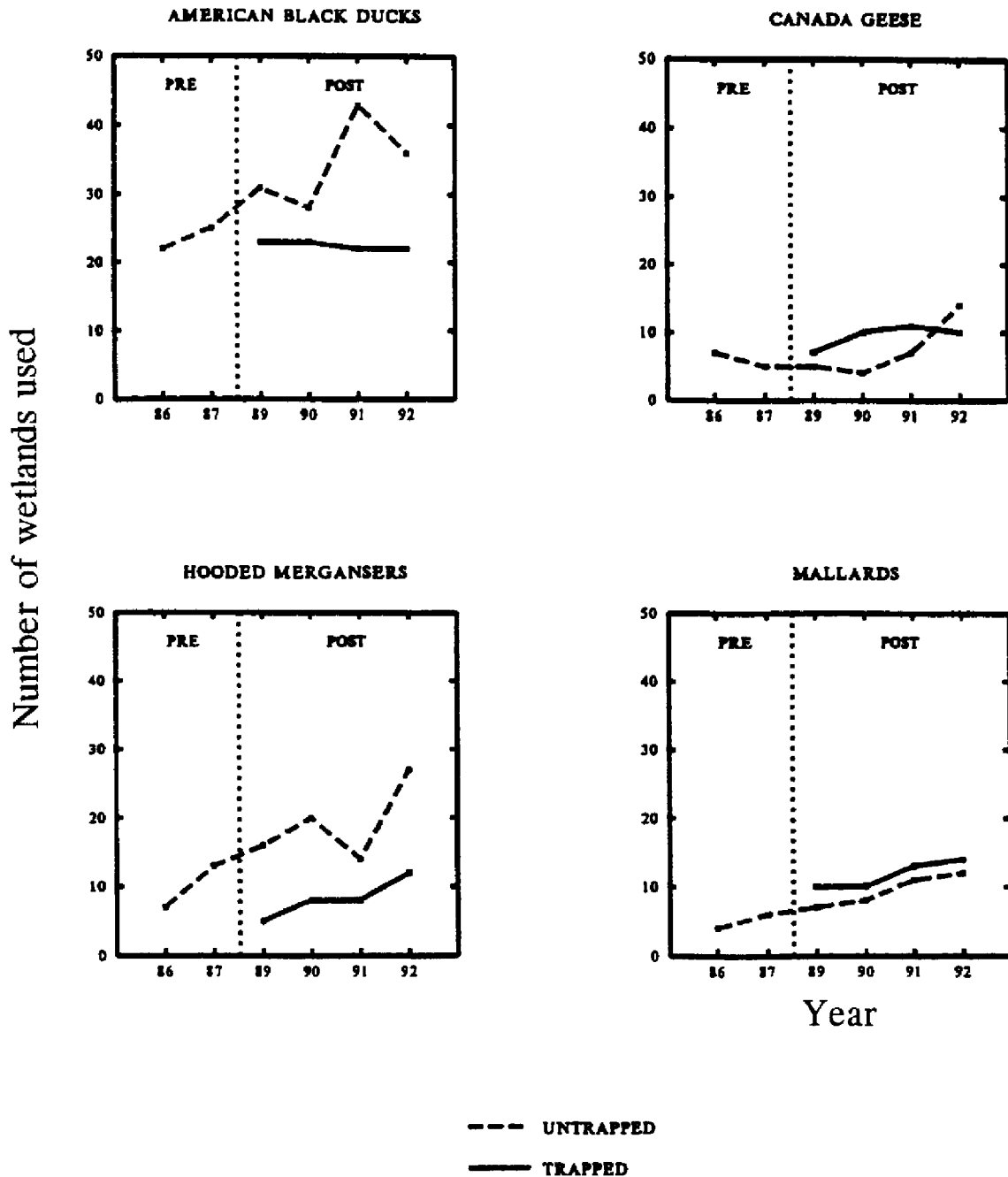


Figure 6. Number of different wetlands used by American black ducks, Canada geese, hooded mergansers, and mallards on the untrapped area during 1986–92 and the trapped area during 1989–92, south-central Maine (PRE = before closure of trapping, POST = after closure of trapping).

lodges and established new colonies (T.C. McCall, Univ. Maine, Orono, unpubl. data). Also, family groups moved to new sites after presumably consuming the available food supply from a wetland.

On the untrapped site, the increase in number of new and refurbished beaver dams and the decline in number of unmaintained dams indicate that beaver were responsible for the increased SWAREA. On the trapped site, the stability in the number of maintained dams

corresponded to the stable density of colonies. The large number of unmaintained dams on the trapped site suggests a potential for increased surface water on the trapped site should the beaver population increase.

Wetland Habitat

We suspect that few potential sites for new wetlands existed on the untrapped site prior to the closure be-



cause most of the increase in surface water on the site resulted from reflooding of wetlands that were previously abandoned by beaver, rather than creation of new ponds. Also, 12 of 14 new wetlands that were created were small (<2 ha) and located in the upper reaches of the watersheds, which indicates that beaver have nearly saturated their habitat on our study site (Johnston and Naiman 1990). Johnston and Naiman (1990) hypothesized that when beaver first move into an area, they colonize sites lower in the watershed where a dam will flood a large area. As beaver reach the capability of the area to support beaver, they move farther up the watershed.

In Minnesota, Johnston and Naiman (1990) reported that an increased number of ponds during a 26-year period in Voyageurs National Park was related to an increase in number of beaver colonies. Similarly, Ermer (1984) determined that a 5-year closure of beaver trapping resulted in a 65% increase in SWAREA on flowages with active beaver colonies, but no increase in surface water occurred until year 3. During our study, closure of trapping resulted in surface water increasing by 36% within 4 years. Factors influencing the degree of wetland expansion from beaver include the availability of beaver food and the topography of the area (Howard and Larson 1985). Greater densities of colonies and wetlands could be expected in areas with less topographic relief where beaver dams flood large areas.

### Waterfowl

Densities of black ducks, Canada geese, and mallards increased slightly during the study, but there was a pronounced increase in numbers of wetlands used by these species. Changes in density and use of wetlands probably resulted from increased wetland habitat following the closure of trapping. More wetlands provide greater isolation for territorial pairs, thereby minimizing time involved in territorial disputes. In Manitoba, Rotella and Ratti (1992a) determined that wetland density influenced the survival of mallard broods and ducklings. Rotella and Ratti (1992b) speculated that broods in areas with low wetland density suffer higher mortality because they move longer distances from nest to wetland and between wetlands. Factors other than breeding habitat also probably contributed to annual variation in the abundance of pairs of some species of waterfowl including weather, harvest, wintering habitat, and disease.

Waterfowl response in this study to changes in habitat can be explained in terms of their habitat requirements. In our study, the increased surface water and area of flooded herbaceous vegetation on the untrapped site probably increased the abundance of inverte-

brates available to waterfowl (Stoudt 1971, Reinecke 1977). There were also increases in area of flooded timber, flooded alder and willow, and emergent vegetation, which increased cover and food for waterfowl (Ringelman 1980, Ringelman and Longcore 1982, Diefenbach and Owen 1989). On the untrapped site, beaver reflooded several large (>3 ha) emergent marshes, creating suitable goose habitat (Bellrose 1980). On our study sites, geese frequently used abandoned beaver lodges surrounded by water as nest sites.

### MANAGEMENT IMPLICATIONS

Waterfowl were used as an indicator of the influence of beaver on wetland habitat in this study, but these areas are important habitat for many species of wildlife (Hodgdon and Hunt 1955, Reese and Hair 1976, Lockmiller 1979, Grover and Baldassarre 1995). Therefore, the primary goal for the management of beaver should be to provide wetland habitat for a variety of wildlife species and secondly to provide a sustained harvest of beaver and a minimal number of damage complaints.

In this study, it required  $\geq 1$  year to begin increasing the density of beaver colonies following closure of an area to trapping, 2 years to begin increasing surface water, and from 3 to 4 years to begin increasing the number of wetlands used by pairs of waterfowl and possibly the density of waterfowl. We recommend that greater densities of beaver colonies be encouraged by trapping fewer colonies. Furthermore, a pattern of opening and closing of townships to trapping should be practiced so that areas are closed for longer periods (3–4 years) and opened for variable periods (2–5 years), assuming that damages by beaver are manageable. Closing areas for longer periods will provide greater opportunity for beaver to increase surface water and influence wildlife. Opening areas for variable periods will ensure a complex of wetlands with some areas flooding and others dewatering. Because beaver harvest is influenced by pelt price, harvest should be more restrictive when pelt price is high and less restrictive when the price is low.

Although closing an area to beaver trapping in this study benefitted wetland habitat and probably enhanced waterfowl and other wildlife, periodic trapping is encouraged because the beaver's food supply of hardwoods cannot support uncontrolled growth of the beaver population. Trapping may help maintain the productivity of wetlands and associated invertebrate populations by periodically removing all beaver from a wetland so that the cycle of flooding and dewatering is repeated more frequently. However, current low prices for beaver pelts and the potential for decreased social acceptance of trapping could make management of beaver more difficult in the future.

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