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"For when we speak of the fur trade, we mean the beaver trade. Other furs were handled; others -- notably the rich sea otter -- were more valuable by far. But the beaver was the root and core of the trade ... Many men died, a continent was explored, an indigenous [human] race degraded and its culture crushed; all because beaver fur, with its tiny barbs, felted up better than any other" (Berry 1961:18).

The habits of beaver (Castor canadensis) allow them to be located and trapped readily, resulting in their extirpation from many areas. Beaver populations have recovered through successful reintroduction and management programs. But the difficulty of preparing beaver pelts for marketing, coupled with low pelt prices, has resulted in high populations of beaver considered to be underharvested in many areas, even though annual harvests are greater now than in recorded history (Novak 1987). This is a reflection of human density as well as beaver density. Any wild animal is labeled a nuisance whenever human conflict is involved. The beaver's same habits render it especially prone to nuisance status even reaching political concern (Payne and Peterson 1986).

Efforts to control beaver populations have been expensive and persistent, largely with marginal and temporary success. Habitat alteration through forest type conversion might be the most effective long-term method of reducing beaver density in some areas, relative to the feasibility of harvesting streamside deciduous trees and shrubs and replacement with closed canopy coniferous plantations. But beaver can subsist on alder (Alnus spp.), and rhizomes of white water lily (Nymphaea odorata) and yellow water lily (Nuphar variegatum), although at lower densities, as well as willow (Salix spp.) (Allen 1983), all of which are likely to occur to some extent with any alteration in habitat type. Moreover, reduced food availability might force beaver colonies to move more often, possibly increasing nuisance complaints. Habitat use seems to depend mainly on physical factors, not food; manipulating forest resources might be of little use in controlling beaver populations (Beier and Barrett 1987).

Most wildlife agencies rely on commercial trappers to help control beaver populations. Harvest intensity and strategy will influence population dynamics, especially of a monogamous, colonial, and territorial species such as beaver.

HABITAT

Population dynamics also are influenced by habitat, with beaver most productive in high quality habitat consisting of stable water levels, valley grades of $\leq$ 6%, valley widths of > 46 m, rock types of glacial till, schist, or granite, and 1.5-2.25 ha/colony/yr of quaking aspen (Populus tremuloides) within 100 m of the shoreline (Retzer et al. 1956, Rutherford 1964). Colony density on streams increases with the degree of bifurcation of the stream channel, the species diversity of vegetation, and the biomass of deciduous trees and shrubs for winter food storage (Boyce 1981a). Beaver eat mainly herbaceous vegetation during ice-free periods, but must store deciduous woody vegetation to eat in winter. Beaver are less dependent on woody vegetation in ice-free southern United States where no browse pile is constructed (Novak 1987), and in the barrens (tundra) where woody vegetation is largely unavailable and the browse pile and lodge consist of water lily rhizomes (N. F. Payne, pers. observ., Jenkins 1981). In the absence of and in addition to aspen, beaver use other deciduous trees and shrubs, especially willow, and even alder, but apparently cannot subsist primarily on conifers (Novak 1987). Beaver are associated with mid-successional stages, benefiting from disturbance caused by fire and logging which eventually results in shade-intolerant beaver foods such as aspen and birch (Betula spp.) (Ingles-Sidorowicz 1982), with a canopy closure of 40-60% best (Allen 1983).

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Beaver have lower densities and survival rates where water levels fluctuate as in large reservoirs, drought-stricken potholes, or brackish tidal areas. They survive by 1) extending the lodge to the retreating water in potholes in aspen parkland (Novak 1987), 2) building canals under ice from lodge to retreating water with wood chip nests around the browse pile in air spaces beneath the ice replacing the lodge, 3) building dams to contain retreating water in reservoirs (Smith and Peterson 1988), 4) building new lodges on an upper story to the old lodge with rising water levels (Courcelles and Nault 1983), or 5) building no permanent lodge on ice-free reservoirs and moving to food sources especially in arid wind-swept areas where wave action and low precipitation limit riparian vegetation (Payne et al. 1976). Areas without streams, with a low water table, and with enough temporary or seasonal runoff from rain and snow melt can support good beaver populations if clay soils are present to prevent percolation of water constrained by beaver dams (e.g., Outer Island, Apostle Islands National Lakeshore, N. F. Payne, pers. observ.).

POPULATION DYNAMICS

Territoriality

Oval-shaped ponds < 1.5 km long contain only 1 colony (N. F. Payne, unpubl. data). Brooks (1977) reported a similar pond size at 2.5 km of shore habitat. Longer ponds especially of irregular shape might contain 2 colonies usually widely dispersed or separated by a bend in the pond with activity areas in opposite directions. Boyce (1981a) reported 0.48 km as the shortest distance between colonies, with an average distance of 1.6 km, but thought that distances > 1 km would be undefended. Even in unharvested populations, many ponds do not contain colonies. A 17.9-km^2 island off north central Newfoundland contained 60 colonies after 5 years of no harvest, of which 90% occurred on only 27% of the 190 lakes and ponds (N. F. Payne, unpubl. data). In northern Canada, 39% of lake and 75% of stream colony sites were unoccupied (Dennington and Johnson 1974). Where relatively flat terrain permits easy movement between ponds, > 1 pond might be included in the territory (Northcott 1964).

Territories on streams vary from about 100 m for new colonies to about 2000 m for old colonies (Bergerud and Miller 1977), averaging about 1000 m long and 180 m overland to the nearest neighbor (Semyonoff 1951, Nordstrom 1972, Bergerud and Miller 1977, Brooks 1977, Busher et al. 1983). Territorial length on streams correlates with the number of beaver-made ponds within the territory and the number of lodges. A colony on a stream increases the length of its territory by building additional dams and ponds, usually downstream of the main dam. Beaver ponds average about 4 ha (Knudson 1962, Novak 1987).

The main function of territorial behavior for beaver seems to be dispersal rather than to regulate the density within food resources (Lack 1966, Bergerud and Miller 1977), which is contrary to 2 prominent theories of self-regulation (Wynne-Edwards 1962, Chitty 1967). Overuse of food by beaver and subsequent decline in density is not prevented by territorial spacing (Bergerud and Miller 1977). Territoriality also reduces intraspecific strife (Aleksiuk 1968). In saturated habitat, dispersers might sustain heavy predation or establish in marginal habitat of low food resources and shallow ponds that might freeze solid during severe winters, causing starvation. Survivors would be available to repopulate in event of a catastrophic decline of the main population (Aleksiuk 1968).

Territories are delineated with scent mounds, which deter dispersing beaver, and reassure colony members (Aleksiuk 1968, Svendsen 1980, Müller-Schwarze and Heckman 1980, Müller-Schwarze et al. 1983, Welsh and Müller-Schwarze 1989). Scent mounds are maintained March-June, or July in northern and alpine regions (Soper 1937, Townsend 1953). Not all colonies have scent mounds; 95% of colonies with neighbors < 500 m had scent mounds, vs. 32% of colonies with neighbors > 500 m (Müller-Schwarze and Heckman 1980). No reports of scent mounds exist for year-round open water areas in southern United States (Novak 1987). In areas such as the Columbia River in the arid shrub-steppe vegetative community of eastern Washington and Oregon, the dammed reservoirs do not freeze, and only limited riparian vegetation exists as beaver food in coves protected from waves (Payne et al. 1976). Beaver cannot maintain stable water levels there, and must remain highly mobile to exploit the limited food resource. This mobile behavior in a territorial species evidently results in frequent intraspecific aggressive encounters, perhaps because territories are not maintained or honored. An unusually high percentage of beaver pelts have severe and numerous wounds, with larger, older beaver often worth less than younger, smaller beaver (e.g., Nordstrom 1972).

Colony Size

Colony density in North America is 0.15-4.6/km^2, varying with habitat quality, territoriality, recruitment, and mortality (Novak 1987). Colony size averages 3.2-9.2 beaver/colony, with the largest colony sizes reported from middle North America (Novak 1987). Nuisance colonies averaged 3.7 (Peterson and Payne 1986), which is low compared to data at similar latitudes. Average colony size depends on the proportion of single, pair, and family colonies in the population (Payne 1982). This proportion has been reported as 14-17% single, 19-24% pair, and 59-66% family colonies (Gunson 1970, Payne 1982, Peterson and Payne 1986). Changes in this proportion will affect census results based on colony counts (Swenson et al. 1983). Young populations will have a smaller average colony size because more pair and single colonies exist, and family colonies are smaller.

The low average age of nuisance colonies reflects dispersal of young beaver into unoccupied territories (Peterson and Payne 1986). The higher the density, the larger the colony size from higher survivorship, and accumulation of non-dispersing subadults (Molini et al. 1981). In dense populations, 42% of the family colonies contain $\geq$ 1 2.5-yr-old; 24% contain 3 beaver $\geq$ 2.5 yrs old (Payne 1982). Yearlings and 2-yr-olds comprised 44% of the beaver in non-nuisance single and pair colonies (Payne 1982), compared to 59% in nuisance single and pair colonies (Peterson and Payne 1986). Beaver 1-3 yrs old comprised 64% of the beaver in non-nuisance single and pair colonies (Payne 1982), compared to 83% in nuisance single and pair colonies (Peterson and Payne 1986). Average age of nuisance colonies is 1.64 yr compared to an average of 2.93 yr for non-nuisance colonies (Peterson and Payne 1986).

Dispersal

Three types of beaver movements apparently exist (Bergerud and Miller 1977, Novak 1987): 1) dispersal of 2-yr-olds, and occasionally yearlings to establish new colonies; 2) movement of the entire colony usually between pond sites within the territory; 3) movement of single adults whose mates were killed. The adult female evidently is the colony leader (Hodgdon and Larson 1973) and evidently holds the colony together, but the adult male will leave if his mate disappears, and the colony will disband (Beer 1955, Miller 1960). Leege (1968) found most movements to be by 2-yr-olds and males, with some by yearlings.

Age ratios of colonies (e.g., Payne 1982) indicate that kits and yearlings usually remain with their parents to disperse in spring just before their 2nd birthday. Dispersal probably is innate (Wilsson 1971). Some yearlings are found in pair colonies (Payne 1982), and breed (Payne 1984a), perhaps an indication of poor quality habitat when yearlings might disperse (Semyonoff 1951, Gunson 1970) due to increased agonistic behavior of dominant beaver in the colony. Even subordinate adults might be forced to disperse if food supplies are limited (Packard 1940, Payne and Finlay 1975). But 2-yr-olds often occur in the parent colony when beaver densities are high, indicating reduced dispersal due to saturated habitat (Novakowski 1965, Bergerud and Miller 1977, Molini et al. 1981, Payne 1982). Indications are that 2-yr-olds delay dispersal when too many other dispersers enter the resident territory and initial dispersal attempts reveal no unoccupied sites (Molini et al. 1981). A delay of 1 yr would increase body size and improve dispersal success when population density is high.

Beaver that breed early will be smaller (Boyce 1981b). Smaller beaver are less likely to survive a long winter due to more rapid consumption of fat reserves and fewer somatic stores (Boyce 1978, 1979). Moreover, in habitat saturated with territorial adults, when food resources might decline, dispersers would sustain high mortality due to intraspecific strife, predation, and seasonal weather conditions if forced to locate in a marginal site of little food or inadequate water (Aleksiuk 1968).

Entire colonies will relocate if water or food conditions become untenable (Rutherford 1964, Gunson 1970). But site abandonment can occur for unknown reasons when food is ample, including the preferred quaking aspen (Retzer et al. 1956, Shelton 1966). A high ratio of inactive to active lodges can reflect overharvesting, or overpopulation if inadequate food supplies or physical features caused frequent recolonization. Inactive lodges tend to accumulate until completely deteriorated or washed out, and are less noticeable from an airplane because no browse pile exists. But in general, the higher the ratio of inactive to active lodges, the greater the indication that the beaver population is at or over its carrying capacity, given no recent history of over-trapping. The lower the habitat quality, the more inactive lodges occur. Colony density of registered traplines in Newfoundland was 0.27/km^2 (0.05-0.46) for 10 management areas of which 8248 km^2 were censused. The inactive:active lodge ratio was 1.71:1 (0.95-10.22) (N.F. Payne, unpubl. data).

<u>Reproduction</u>

A 1:1 sex ratio is needed for maximum productivity of this monogamous species which is unable to seek mates outside the colony during estrus when ponds and streams are frozen. Beaver mate during late October-March in the southern United States, January-March in middle North America, and February-March in northern and montane regions (Novak 1987). They are polyestrous, with 2-4 estrus cycles of 7-15 da each, during which the dominant female is receptive for about 12 hrs. The gestation period is 105-107 da. Litter sizes vary regionally in North America somewhat, but not substantially: Southeast 2.4, Northeast 3.8, Midwest and south Canadian prairies 4.7, West 3.2, North 3.3 (Novak 1987). Kits comprise 16-66% of beaver populations, yearlings 10-43%, and adults 8-66% in various areas of North America (Novak 1987).

Beaver productivity follows the typical pattern of low average litter size and prequency rates for young and old beaver, with peak production during middle years (Payne 1984a). Pregnancy is 70% for adults ($\geq$ 2.5 yrs), or 62% including yearlings. Age-specific pregnancy rates can vary substantially, and thus have more impact on production than age-specific litter size. Age-specific pregnancy seems to be 0% for kits, 25% for yearlings, 33% for 2-yr-olds, 60% for 3-yr-olds, and 90% for older beaver (Payne 1984a, Novak 1987). Yearling breeding has been reported at 40-54% (Lyons 1979, Parsons and Brown 1979), perhaps in response to high density when more yearlings might disperse due to poor quality habitat (Semyonoff 1951, Gunson 1970). Lyons (1979) reported 87% pregnancy of adults. The fecundity rate is highest during ages 5-13 yrs. The reproductive value, which combines fertility with survivorship, is highest during ages 5-9, but contribution to the net reproductive rate seems highest for 3.5-yr-olds and yearlings when they comprise a high percentage of dominant females (Payne 1984a, b).

In nuisance colonies, 13% of yearlings and 87% of older females are pregnant, including 88% for 2.5-yr-olds (Peterson and Payne 1986). The higher percentage of 2.5-yr-olds breeding in nuisance colonies compared to non-nuisance colonies might reflect their dispersal to sites vacated regularly through nuisance trapping and their availability as breeders (Payne 1984a). The lower rate for 1.5-yr-olds might reflect high prenatal mortality (80%) in beaver where energy must be diverted to the body growth still in progress (Peterson and Payne 1986). In fact, low pregnancy rates of 2.5- and 3.5-yr-olds are consistent with the energy budget allocated then to body growth, with little or no growth occurring later in northern latitudes (Novakowski 1965, Aleksiuk and Cowan 1969a, b, Boyce 1981b). Also, low pregnancy rates might reflect the difficulty dispersing 2- and 3-yr-olds have in finding territories and mates. When beaver densities are high, only marginal habitat with unsuitable amounts of water and food would be available for territories. At low densities, suitable habitat might be available for establishing territories, but mates might not be readily available.

Evidence suggests beaver productivity is density-dependent (Pearson 1960, Gunson 1970, Boyce 1974, Parsons and Brown 1979, Payne 1984a). Few or no yearlings breed when > 40% of the potential colony sites are occupied (Parsons and Brown 1979). Resorption rates seem higher in areas of high density or poor habitat (Rutherford 1964, Gunson 1970). Because of the large number of yearlings in the population normally, even low percentages of breeding yearlings will contribute substantially to population growth.

Mortality

Annual mortality of stationary beaver populations, trapped or untrapped, is about 26-30% (Boyce 1974, Bergerud and Miller 1977, Lyons 1979, Payne 1984b). Mortality for adults only (≥ 2.5 yrs) is 30-32% (Gunson 1970, Payne 1984b). The pattern of age-specific mortality seems to show that mortality during the 1st yr is minimal (Payne 1984a, Novak 1987), due to protection of kits within the parent colony. During the 2nd yr mortality is about 40%, as yearlings wander further from the parent lodge and some disperse. Yearlings are still small enough (9-13 kg) to be preyed upon readily. Mortality during the next 2 yrs also is about 40% as beaver disperse, locate suitable territories, and continue body growth. After completion of body growth, mortality is about 20% for 4.5- to 10.5-yr-olds, increasing thereafter. Total annual mortality is similar for both sexes (Payne 1984a).

The mortality pattern can vary. Mortality of kits can be 31-49% (Henry and Bookhout 1969, Gunson 1970, Nordstrom 1972, Boyce 1974, Novak 1987).

Harvest mortality is 13-70% (Henry and Bookhout 1969, Novak 1977, 1987, Boyce 1981b, Payne 1984b). Natural mortality in harvested populations ranges 0-24%, depending on harvest intensity (Payne 1984b). Harvest mortality seems compensatory with natural mortality. Natural mortality is imposed through limited predation (mainly wolves in summer), tularemia, starvation, and intraspecific strife (Novak 1987).

HARVEST RESPONSE

Harvested beaver populations have lower density than unharvested populations do (Nordstrom 1972, Parsons and Brown 1978). Reproduction evidently can replace annual mortality of 30%. Probably higher mortality can be balanced with compensatory reproduction, for 30% harvests in Ontario seem to produce sustained yields and 43% on excellent habitat is excessive (Novak 1987). Trapping can be distributed throughout the entire trapline, or the trapline can be divided into 2 or 3 sections with each section trapped heavily in rotation. High harvest rates the 1st yr decrease the density of colonies by a smaller amount than lower harvest rates in following years (N. F. Payne, unpubl. data).

Changes in the proportion of single, pair, and family colonies in the population will affect age structure and trapping results. More adults will appear in the harvest if more pair and single colonies occur, especially if only 1 or 2 beaver are trapped/colony (Boyce 1974, Payne 1980, 1982). Average colony size is larger in unharvested than in harvested populations (Nordstrom 1972, Payne 1982), unless harvests are somehow restricted to single and pair colonies (i.e., those colonies with small lodges and browse piles), with most family colonies unharvested.

Leaving most family colonies unharvested would allow many dominant females to survive to their most productive age (5-13 yrs) to produce the highest number of dispersing beaver to reoccupy trapped out territories. Trapping before the winter breeding season will remove some dominant females and males, leaving unmated surviving dominant females barren that year, thus reducing population growth unless subordinates assume the reproductive roles. Yearling breeding is more prominent in harvested than in unharvested populations (Nordstrom 1972, Boyce 1974, Lyons 1979), when some yearlings evidently become reproductively active in the absence of an adult of the same sex (Payne 1984a, Brooks et al. 1980), or when some yearlings disperse and establish colonies (Payne 1982). Yearling breeding increases to 11-44% when beaver populations are harvested (Henry and Bookhout 1969, Gunson 1970, Nordstrom 1972, Lyons 1979, Payne 1984a). Litter size can increase even the 1st yr after trapping (Nordstrom 1972, Payne 1984a). Fecundity appears density-dependent, although harvests of 70% depress embryo production (Novak 1987).

Harvest season length (Erickson 1981) and market values (Payne and Peterson 1986, Novak 1987) influence beaver harvests. Inclement weather generally is not influential by itself, because of individual variation in trapping effort during such weather (Erickson 1981). Beaver harvests do not increase with increasing beaver populations, unless pelt values increase (Erickson 1981). If pelt prices remain relatively constant, the beaver harvest can be predicted generally (Erickson 1981): Beaver Harvest = 1915.9 + 27.8 (no. days of trapping season). Reduced seasons presumably reduce the harvest, but the reduction must be substantial, perhaps > 50%, to compensate for harvest effort concentrated into the shorter season (Erickson 1981). Moreover, increased pelt prices and reductions in season length for other furbearers might influence harvests of beaver.

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