Ann. Zool. Fennici 29:47–55
Helsinki 21 April 1992
ISSN 0003-455X

The importance of beaver ponds to waterfowl broods: an experiment and natural tests

Petri Nummi

Nummi, P., Finnish Game and Fisheries Insititute, Game Division, Turunlinnantie 8, SF-00930 Helsinki, Finland. — Present address: University of Helsinki, Department of Applied Zoology, SF-00710 Helsinki, Finland

Received 8 February 1991, accepted 31 May 1991

The use of flooded water bodies by duck broods was studied in one simulated beaver-pond and eight beaver-influenced ponds. Brood censuses were made both before and during inundation in these areas, and eight unaffected ponds were used as controls. In the man-made flowage, the distribution and biomass of wetland plants and the density of available aquatic invertebrates were studied. In the beaver-influenced ponds, the use by waterfowl broods was significantly greater during flooding than before inundation; no changes occurred in the control areas. In the first year of inundation, the simulated flowage produced a great amount of duck food in the water column — mainly large cladocerans. The density of benthic invertebrates increased during the second year of flooding and remained high during the third. The number of emergent insects was highest in the second year of inundation. The results of the study suggest that in barren regions beaver ponds, with their prosperous food regime, provide important habitats for rearing waterfowl broods.

1. Introduction

The ecological role of beaver has received considerable attention in North America (Knudsen 1962, Naiman et al. 1986), where most of the research has focused on the relationships between beaver and waterfowl (e.g. Beard 1953, Speake 1956, Nevers 1968, Renouf 1972, Diefenbach & Owen 1989) and between beaver and trout (Huey & Wolfrum 1956, Gard 1961). In Eurasia, only minor studies have been made on the effect of beaver on waterfowl (Rudqvist 1977, Nummi 1984).

Much of the earlier work has concentrated on explaining the importance of cover to waterfowl broods in beaver ponds and, therefore, there is not much information about beaver flowages as producers of invertebrate food for ducks. Protein-rich invertebrates are important to breeding females and their broods (Sugden 1973, Krapu 1974, Street 1977, Reinecke & Owen 1980, Swanson et al. 1985; see also Nummi 1985). Nor is the timing of the waterfowl brood response to beaver flooding well documented.

In this paper I shall describe the development of the vegetation structure, food supplies, and their use by ducks in a simulated beaver pond over a three-year period. Against this background, I shall then test the hypothesis that the use of natural ponds by duck broods increases after damming by beaver. I collected brood data from the same ponds before and during beaver occupation, and compared these with unaffected controls. Earlier studies have only compared beaver ponds to other kinds of habitat.

2. Study area and methods

The study was conducted in the barren watershed area of Evo (61°N, 25°E) in southern Finland and in Pitkäpohja (61°N, 29°E), a more productive area in eastern Finland. In these areas, a long-term study of waterfowl habitat selection is in progress. The waters under study consist of about 90 small lakes and ponds, which are mostly oligotrophic; of these, 16 are the main focus of this work. The most common waterfowl species nesting in the study areas are the mallard *Anas platyrhynchos* (L.), teal *A. crecca* (L.), wigeon *A. penelope* (L.) and goldeneye *Bucephala clangula* (L.). The species of beaver living in southern and eastern Finland is *Castor canadensis* (Kuhl).

The experimental work at Evo was started in June 1984 in Saukonoja Creek in two sections situated 300 m apart. The lower was flooded and the upper was used as a control. The artificial damming took place in October 1984 and the area of the inundated floodplain was 1 ha. The water level rose about 50 cm.

2.1. Invertebrate sampling

During June, emerging insects were collected in four floating hood traps from the flowage and from the control; the hood traps were made of a ring-shaped plastic tube surmounted by an arch supporting a net (mesh size 0.5 mm). Each trap collected insects from an area of 0.5 m^2. The hood traps were emptied with a small vacuum cleaner. In the flowage in 1985–1987 and in the control in 1985–1986, the traps were set for 17 days (in each year the trapping periods were 5×3 days plus 2×1 day). In 1987, the control had only two trapping periods of one day, and in 1984 the traps were set for only four periods of one day in both sections.

Free-swimming invertebrates and species living on the submerged vegetation were sampled with a sweep net (aperture 177 cm^2, mesh size 0.5 mm) in the littoral portion of the flowage between 25 June and 2 July in 1985–1987. For each sample, a water volume of about 33 litres was swept in the surface layer; four, eight and twelve samples were taken in 1985, 1986 and 1987, respectively. A core sampler (15.2 cm^2) (Hakala 1971) was used to collect benthic invertebrates in the littoral zone at the flowage at depths of 5–15 cm from 14 to 25 July. The samples were sorted with an automatic sieve (smallest mesh size 0.5 mm) and the animals were then picked out by hand. Thirty samples were taken each year (1984–1987).

2.2. Analyses of vegetation

Two line transects of 70 m and 55 m were laid at random across the flowage. Between 26 July and 10 August in 1985–1987, records were made at intervals of 0.5 m along the transects of the frequency of occurrence of macrophytes and of shrubs under a height of 0.5 m. In this way, a maximum of 250 sample intervals was measured.

In the years 1984–1987, the above-ground biomass of macrophytes in the floodplain was determined by harvesting the plants from 20 quadrats of 0.25 m^2 selected at random along the transect. The samples were dried for 1–2 days at 40 °C before the weighing. Leaf litter from trees in the flowage was also collected in 12 nine-litre buckets attached to floating boards. Collection took place in a two-month period from mid-August to mid-October, and the buckets were emptied every second or third week. The litter samples were dried in the same way as the macrophytes.

2.3. Waterfowl observations

The number of waterfowl broods in the experimental flowage was rercorded during observation periods of 15 and 60 minutes. These records were made from an observation tower about every second day from mid June to early August in 1984–1987 at 0700–0900 hours or 1900–2100 hours, which are active feeding periods of duck broods in the study area. The number of birds or broods seen per hour was then used as an index describing the use of the area by the birds. Broods of the same species could be separated quite reliably on the basis of their age (Pirkola & Högmander 1974) and the number of ducklings.

To test whether the use of wetlands by duck broods is greater after beaver damming, additional brood counts were made during three-year periods from eight beaver-influenced ponds in Evo (seven ponds) and in Pitkäpohja (one pond) in 1984–1990. In each wetland, either point counts or round counts were used on all visits (methods described in Koskimies & Väisänen 1991). The wetlands were censused 1–4 times per season in June and July. The average values of all censuses were used in comparisons of brood use before (1 or 2 years) and during (1 or 2 years) beaver occupation. Comparisons were made with Wilcoxon's signed ranks test. For each of the eight beaver ponds, there was one control area (seven in Evo and one in Pitkäpohja) of the same habitat type. The habitats used resembled the beaver areas as much as possible, because bird densities may vary from year to year in different kinds of habitats. The controls were the nearest neighbours of the beaver areas in a principal component analysis (PCA) gradient representing eutrophy-oligotrophy. The PCA was based on vegetation descriptions of all the water bodies (89) in the study areas (details in Pöysä & Nummi 1992; see also Pöysä & Nummi 1990).

To test for species differences in the use of the beaver ponds, the proportion of teals, mallards and goldeneyes in the seven beaver-influenced ponds of Evo was compared to the total brood data (minus beaver pond data) for those species in the area.

3. Results

3.1. Experimental pond

3.1.1. Invertebrates

Emerging insects

The number of emerging insects peaked during the second year of flooding (1986) (Figs. 1 and 2A). Large midges (Chironomidae, *Chironomus* spp.) in particular were more numerous than in the previous two years or the control area. Mayflies (Ephemeroptera) were also abundant in 1986 during their short emergence peak at the beginning of June.

In 1985, the number of emerging midges had already started to increase. By 1987 the number of adult midges was again low.

Free-swimming and benthic invertebrates

Invertebrates were most abundant in the water column ($P < 0.01$, Mann-Whitney U-test) in 1985 (Fig. 2B). During the first year of inundation, most of the invertebrates (84 %) were waterfleas (Cladocera) of the relatively large-sized genus *Eurycercus*.

The density of bottom-dwelling invertebrates in the littoral zone did not increase until 1986 ($P < 0.01$) (Fig. 2C). Most of this increase (40 % of total) was due to water-lice *Asellus aquaticus*, but midge larvae had already increased slightly in 1985. In 1987 the benthic invertebrate density was at the same level as in 1986. The densities of invertebrates on the creek bed showed the same trend as the densities of the littoral macrobenthos (Nummi 1989).

3.1.2. Vegetation

Biomass of herbaceous plants and dead leaves

Before flooding in 1984, the biomasses of herbaceous plants and leaf litter from the flood plain trees were both about 190 g/m^2 (Fig. 3). The standing crop of herbaceous plants decreased considerably during the first year of inundation and this is reflected in the total biomass of vegetative matter. The amount of autumnal leaf litter, however, was still about 120g/m^2 in 1985.

Occurrence of herbaceous plants and shrubs

In 1985, there were few sections without plant contact (18 %) on the transect lines. In 1986, the number of open sections increased slightly (27 %), but plants were evenly distributed throughout the flowage (Nummi, unpubl.). In 1987, the vegetation became sparser (41 %), in spite of the

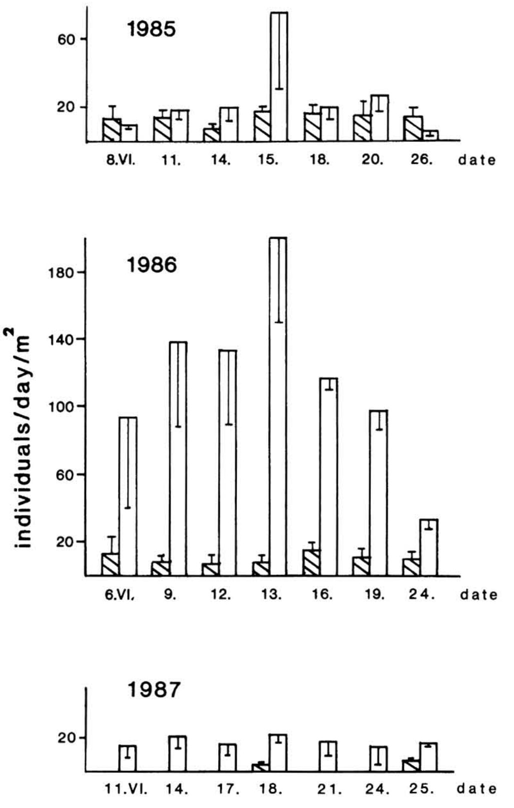

Fig. 1. The number of emerging insects (mean +1 *SE*) in June in the experimental flowage (open columns) and in the control section of the creek (shaded columns) during 1985-1987 (for each column, $n = 4$). The creek was dammed in October 1984.

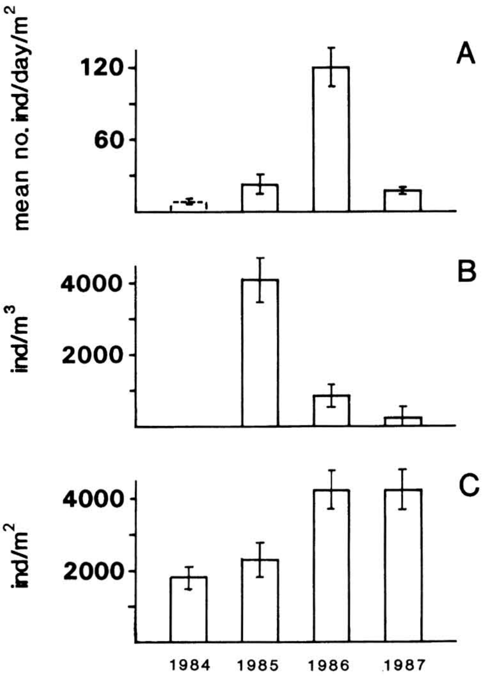

Fig. 2. The number of invertebrates (mean ± *SE*) in the experimental flowage during 1984–1987. Flooding was done in October 1984. — A. The mean number of emerging insects per day during 17 days in June (in 1984 only during 4 days) (hood traps, 7 collections, $n = 4$ for each collection; in 1984 only 2 collections). — B. Density of free-swimming invertebrates in sweep net samples between 25 June and 2 July in 1985 ($n = 4$), 1986 ($n = 8$) and 1987 ($n = 12$). — C. Density of benthic invertebrates in mid-July during 1984–1987 (yearly sample size 30).

fact that fallen willows added more contacts in 1987 than in 1985 or 1986.

3.1.3. Waterfowl

The number of waterfowl broods recorded per hour was greatest during the first and second years of flooding (Table 1). During the third year, the pond was used less by broods than during the first two years ($P < 0.05$, χ^2-test), but more than in the year before flooding ($P < 0.01$). Because of the small size of the flowage, the actual number of broods using it was small: probably four in 1985 and six in 1986 and 1987.

Teal broods were seen most often in the flowage. During the first year of flooding, when 18 records were made of teal broods, there were only three each of mallards and goldeneyes ($P < 0.01$). Teal ducklings also seemed to remain in the flowage until fledging.

3.2. Waterfowl in beaver-influenced ponds

After damming by beaver, the use of the eight ponds by waterfowl broods was significantly higher than before inundation ($P < 0.005$, Wilcoxon's signed ranks test; Table 2). In the controls, the use by broods did not change

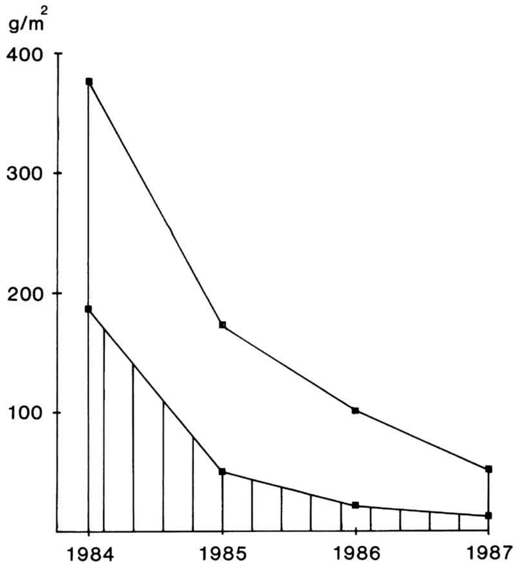

Fig. 3. Biomass of leaf litter fall in autumn (open area, yearly sample size = 12) and macrophytes (ruled area, yearly sample size = 20) per square meter during 1984–1987 in the experimental flowage, flooded in October 1984.

($P > 0.10$) during the same period (Table 2). Half (51 %) of the broods in beaver ponds were teals, over one third (38 %) goldeneyes and 11 % mallards (Table 3). The proportion of teals in beaver ponds was higher ($P < 0.01$, G-test) than in the area of Evo in general (31 %).

4. Discussion

Waterfowl broods seem to use intensively beaver-influenced ponds as well as man-made flowages. In the following discussion I will specify the factors that are responsible for the rapid response of broods to the creation of inundated wetland. Although there was only one replicate of the experimental work (for more detailed information on e.g. invertebrates, see Nummi 1989), other studies have shown similar trends in such processes as thinning of macrophyte stands (Danell & Sjöberg 1982, Murkin & Kadlec 1986) and colonization by invertebrates (Smirnov 1962, Sjöberg & Danell 1983).

4.1. Colonization by invertebrates and their use as duck food

During the first year of flooding, the invertebrates (mainly water-fleas) in the simulated beaver pond were produced mainly in the water column (Fig. 2b). The food items were relatively small, which is typical of the first phase of invertebrate succession in flowages (Britton 1982). Young ducklings are able to take invertebrates from the water surface (Chura 1961, Sugden 1973, Pehrsson 1979, Nummi 1985). Water-fleas, numerous in the simulated pond in the first year of inundation, are known to be the customary food of young ducklings (Collias & Collias 1963, Bengtson 1971). Even relatively small fledged teals eat large amounts of water-fleas (Nummi 1990). The foraging behaviour of adult teals also suggests great use of free-swimming invertebrates; teals feed much more often at a depth of 0–5 cm than, for example, mallards (Pöysä 1983). In experimental conditions, blue-winged teals *Anas discors* feeding solely on water-fleas have survived and even reproduced (Swanson et al. 1974).

In the second year of inundation, the number of free-swimming invertebrates was much lower. Conversely, the number of emerging insects and the density of benthic invertebrates had increased (Figs. 1 and 2A, 2C). As in the study by Sjöberg & Danell (1983), the first benthic invertebrate to attain high densities was *Asellus*. Emerging insects are an important part of the nutrition of downy young (Bengtson 1975, Street 1977, Sjöberg & Danell 1982). Ducklings of older age classes subsist mainly on benthic invertebrates,

Table 1. Number of observations of waterfowl per hour before and after damming in the experimental flowage area during 1984–1987 (observation periods of 15 min and 60 min).

Year	Effort hrs	Broods observ.	Observations / hr broods	adults	ducklings
1984	12.8	1	0.1	0.1	0.5
Dam					
1985	14.3	24	1.7	1.7	8.8
1986	13.0	24	1.8	2.0	9.8
1987	18.8	19	1.0	1.5	5.9

e.g. isopods and amphipods, midge larvae and snails (Chura 1961, Sugden 1973, Krapu & Swanson 1977, Danell & Sjöberg 1980). These also constitute a substantial part of the diet of adult ducks in the breeding season (Krapu 1974, Swanson & Meyer 1977, Swanson et al. 1979, Reinecke & Owen 1980).

As an impoundment becomes older, its value for young ducklings decreases. However, older birds which feed by up-ending still benefit from the benthic invertebrates produced in the relatively shallow water of flowages (Danell & Sjöberg 1982, Nummi 1984, Diefenbach & Owen 1989).

4.2. The role of vegetation as invertebrate food

The high production of invertebrates in the flooded area may be attributed to the presence of inundated macrophytes and leaf litter (Kadlec 1962, Mundie et al. 1973, Whitman 1976, Murkin & Kadlec 1986). The invertebrates feed on the litter itself and on the microbes, fungi and epiphytic algae that live on it (Andersson & Sedell 1979, Moss 1980, Nelson & Kadlec 1984). Invertebrates that live in open water or among stands of vegetation can also benefit from accumulations of litter. During decomposition, the litter becomes a source of fine particulate organic matter, which collector invertebrates can filter from the water (Nelson & Kadlec 1984).

In my experimental pond, the autumnal input of leaves (Fig. 3) may have played an important role in the production of invertebrates. Flowages surrounded by trees also receive additional inputs from the canopies also during other parts of the year, e.g. woody debris, pollen and flower parts (Anderson & Sedell 1979). The biomass of herbaceous plants was high only before the flooding in 1984 (Fig. 3). Many of the plants initially flooded decay fairly rapidly: 50–100 % in one year, 30–80 % in half a year (Mason & Bryant 1975, Hodginson 1975, Danell & Sjöberg 1979, Danell & Andersson 1982).

4.3. Beaver ponds and beaver-influenced ponds as feeding habitats for ducklings

Although the biomass of herbaceous plants decreased rapidly, the vegetation was evenly distributed throughout the experimental pond in the first years of inundation (Nummi, unpubl.). Thus, the young ducklings had good opportunities to chase insects on the vegetation — also some distance from the shore line. Pehrsson (1979) has suggested that a well-vegetated shore line is in fact a dangerous habitat for ducks because of the terrestrial predators, but that ducklings move along the shore vegetation because of the abundant food resources available there. In open water, however, ducklings can be detected by raptorial birds. In newly flooded ponds, canopies of shrubs and trees are often present and give protection from raptors. The use of beaver ponds by wood ducks *Aix sponsa* has been associated with abundant shrub cover (Hepp & Hair 1977, Brown & Parsons 1979). In my experimental pond, both the birches and willows were in good leaf in

Table 2. Average number of broods in beaver-influenced ponds and unaffected controls before and after damming. Number of censuses in parenthesis.

Beaver-influenced ponds: brood number higher after damming ($P < 0.005$, Wilcoxon's matched-pairs signed ranks test).

Pond nr.	1	2	3	4	5	6	7	8
Before	– (2)	– (8)	– (1)	0.25 (4)	– (8)	– (4)	0.25 (4)	1.0 (4)
After	1.80 (5)	1.75 (4)	0.88 (8)	1.13 (8)	0.75 (4)	0.63 (8)	0.75 (8)	1.25 (8)

Unaffected control ponds: brood numbers do not differ between the two periods ($P > 0.10$).

Pond nr.	1	2	3	4	5	6	7	8
Before	– (2)	0.25 (8)	– (1)	– (4)	0.63 (8)	– (4)	1.0 (4)	0.25 (4)
After	– (5)	– (4)	0.25 (8)	– (8)	– (4)	– (8)	3.25 (8)	– (8)

1985 and in 1987 the willows were still in good condition (Nummi 1989).

Young ducklings chasing insects on the vegetation move rapidly because the insects attempt to escape. Each duckling, therefore, requires an undisturbed feeding patch. In an evenly vegetated flowage, the brood can advance on a wide front. Beaver-affected areas could, indeed, be a better feeding habitat for ducklings than the narrowly vegetated shores typical of oligotrophic areas, even if the invertebrate densities in these habitats do not differ.

During cold weather, when new insects are not emerging, small ducklings can also benefit from emergent vegetation. Adult midges, for example, are captured easily on the shoots when their mobility is reduced by low temperatures (Sjöberg & Danell 1982). The canopies of trees growing in the flowage can act in the same manner. Mason & MacDonald (1982) have shown that the number of invertebrates falling into a stream from trees is substantial; the peaks of invertebrate input were usually associated with stormy weather.

4.4. Impoundments and waterfowl production

In areas of low productivity and stable water levels, one of the major factors regulating duck populations is the lack of suitable food for broods (Patterson 1976). In these areas breeding pairs tend to use a large part of the available water area, whereas the broods are concentrated in more eutrophic waters (Patterson 1976, McNicol et al. 1987), where invertebrate production is high (Talent et al. 1982, Pehrsson 1984). Both beaver-affected areas and man-made flowages provide this kind of eutrophic habitat. Teals in particular start to use them rapidly (Table 3, see also Sjöberg & Danell 1983), and seem able to complete their whole development in a single flowage; the sedentary nature of teal broods has also been noted in peatlands (Fox 1986).

Table 3. The number of broods of different waterfowl species (wigeon omitted because of scarcity of data) in beaver ponds of Evo and in the area in general (minus beaver pond data). The two distributions differ from each other ($P < 0.01$, *G*-test).

	Teal	Mallard	Goldeneye
Beaver ponds	24	5	18
Evo area	28	29	62

Impoundments are known to remain productive for 3–6 years (Kadlec 1962, Nevers 1968, Danell & Sjöberg 1982, Nummi 1984). This means that in oligotrophic areas beaver ponds often do not become unproductive because the beavers usually deplete their food resources during that time and move away (Lahti & Helminen 1974, pers. obs.). In impoundments created by man, however, the production will eventually decrease and a water-level drawdown is needed (Whitman 1976).

As regards the size of man-made flowages, it may be more profitable to create a number of small impoundments instead of a large one — especially if they can be spaced relatively far apart among oligotrophic lakes, and, if they have good connections with other waters. At least two advantages could be gained in this way. First, as many breeding hens as possible would have access to good feeding sites during spring without harassment (see McKinney 1965, Patterson 1976, Hill 1984). Second, after hatching the broods would not have to travel long distances in order to find a suitable habitat. The highest duckling mortality occur before the ducklings are two weeks old (Talent et al. 1982), and overland movements can have an adverse effect on ducklings (Keith 1961, Ball et al. 1975). Impoundments should probably not be under 0.5 ha in size — even though the pair densities might be higher in smaller water bodies (Dzubin 1969, Lokemoen 1973) — because broods do not favour very small ponds (Lokemoen 1973, Hepp & Hair 1977). However, beaver population management has been shown to be much more economical than the creation of man-made impoundments (Ermer 1984).

Acknowledgements. I thank Kjell Danell, the late Olli Järvinen, Matti K. Pirkola and Hannu Pöysä for encouragement and advice during the study. I am also indebted to Hannu Pöysä for data from Pitkäpohja. I am grateful to Heikki Koivunen for making everything possible in the field and to Marcus Wikman for helping with the computations. Critical comments on earlier drafts of the manuscript were made by Kjell Danell, Duane R. Diefenbach, Olli Järvinen, Harto Lindén, Hannu Pöysä and an anonymous referee. Financial support for this work was given by the Finnish Cultural Foundation, Finnish Game Foundation, Hunters' Central Organization and the Foundation for Research on Natural Resources in Finland.

References

Anderson, N. H. & Sedell, J. R. 1979: Detritus processing by macroinvertebrates in stream ecosystems. — Ann. Rev. Entomol. 42:351–377.

Ball, I. J., Gilmer, D. S., Cowardin, L. M. & Riechmann, J. H. 1975: Survival of wood duck and mallard broods in north-central Minnesota. — J. Wildl. Managem. 39:776–780.

Beard, E. B. 1953: The importance of beaver in waterfowl management at the Seney National Wildlife Refuge. — J. Wildl. Managem. 17:398–436.

Bengtson, S.-A. 1971: Food and feeding of diving ducks breeding at Lake Myvatn, Iceland. — Ornis Fennica 48:77–92.

— 1975: Food of ducklings of surface feeding ducks at Lake Myvatn, Iceland. — Ornis Fennica 52:1–4.

Britton, R. H. 1982: Managing the prey fauna. — In: Scott, D. A. (ed.), Managing wetlands and their birds: 92–97. Int. Waterfowl Res. Bureau.

Brown, M. K. & Parsons, G. R. 1979: Waterfowl production on beaver flowages in a part of New York. — N. Y. Fish & Game J. 26:142–153.

Chura, N. J. 1961: Food availability and preferences of juvenile mallards. — Trans. N. Amer. Wildl. Conf. 26:121–134.

Collias, N. E. & Collias, E. C. 1963: Selective feeding by wild ducklings of different species. — Wilson Bull. 75:6–14.

Danell, K. & Andersson, Å. 1982: Dry weight loss and colonization of plant litter by macroinvertebrates: plant species and lake types compared. — Hydrobiologia 94:91–96.

Danell, K. & Sjöberg, K. 1979: Decomposition of Carex and Equisetum in a northern Swedish lake: dry weight loss and colonization by macro-invertebrates. — J. Ecol. 67:191–200.

— 1980: Foods of wigeon, teal, mallard and pintail during the summer in a northern Swedish lake. — Viltrevy 11:141–167.

— 1982: Successional patterns of plants, invertebrates and ducks in a man-made lake. — J. Appl. Ecol. 19:395–409.

Diefenbach, D. R. & Owen, R. B. 1989: A model of habitat use by breeding American black ducks. — J. Wildl. Managem. 53:383–389.

Dzubin, A. 1969: Comments on carrying capacity of small ponds for ducks and possible effects of density on mallard production. — Can. Wildl. Serv. Rep. 6:138–160.

Ermer, E. M. 1984: Analysis of benefits and management costs associated with beaver in western New York. — N. Y. Fish Game J. 31:119–132.

Fox, A. D. 1986: The breeding Teal (Anas crecca) of a coastal raised mire in central West Wales. — Bird Study 33:18–23.

Gard, R. 1961: Effects of beaver on trout in Sagehen Creek, California. — J. Wildl. Managem. 25:221–242.

Green, W. E., MacNamara, L. G. & Uhler, F. M. 1964: Water off and on. — In: Linduska, J. P. (ed.), Waterfowl tomorrow: 557–568. U. S. Dept. Inter., Washington, D. C.

Hakala, I. 1971: A new model of the Kajak bottom sampler, and other improvements in the zoobenthos sampling technique. — Ann. Zool. Fennici 8:422–426.

Hepp, G. R. & Hair, J. D. 1977: Wood duck mobility and utilization of beaver pond habitats. — Proc. Ann. Conf. S. E. Assoc. Fish & Wildl. Agencies 31:216–225.

Hill, D. A. 1984: Population ecology in the mallard Anas platyrhynchos L. — J. Anim. Ecol. 53:191–202.

Hodginson, I. D. 1975: Dry weight loss and chemical changes in vascular plant litter of terrestrial origin, occurring in a beaver pond ecosystem. — J. Ecol. 63:131–142.

Huey, W. S. & Wolfrum, W. H. 1956: Beaver-trout relations in New Mexico. — Prog. Fish-Culturist 18:70–74.

Kadlec, J. A. 1962: The effects of a drawdown on a waterfowl impoundment. — Ecology 43:267–280.

Keith, L. B. 1961: A study of waterfowl ecology on small impoundments in southeastern Alberta. — Wildl. Monogr. 6. 88 pp.

Knudsen, G. J. 1962. Relations of beaver to forest, trout and wildlife in Wisconsin. — Wisc. Cons. Dept. Tech. Bull. 25. 52 pp.

Koskimies, P. & Väisänen, R. A. 1991: Monitoring bird populations. — Zool. Museum, Finnish Museum Nat. Hist. 144 pp.

Krapu, G. L. 1974: Foods of breeding pintails in North Dakota. — J. Wildl. Managem. 38:408–417.

Krapu, G. L. & Swanson, G. A. 1977: Foods of juvenile, brood hen, and post-breeding pintails in North Dakota. — Condor 79:504–507.

Lahti, S. & Helminen, M. 1974: The beaver Castor fiber (L.) and Castor canadensis (Kuhl) in Finland. — Acta Theriol. 19:177–189.

Lokemoen, J. T. 1973: Waterfowl production on stock-watering ponds in the northern plains. — J. Range Managem. 26:179–184.

Mason, C. F. & Bryant, R. J. 1975: Production, nutrient content and decomposition of Phragmites communis and Typha angustifolia. — J. Ecol. 63:71–95.

Mason, C. F. & Macdonald, S. M. 1982: The input of terrestrial invertebrates from tree canopies to a stream. — Freshw. Biol. 12:305–311.

McKinney, F. 1965: Spacing and chasing in breeding ducks. — Wildfowl Trust Ann. Rep. 16:92–106.

McNicol, D. K., Bendell, B. E. & Ross, R. K. 1987: Studies of the effects of acidification on aquatic wildlife in Canada: waterfowl and trophic relationships in small lakes in northern Ontario. — Can. Wildl. Serv. Occ. Pap. 62. 76 pp.

Moss, B. 1980: Ecology of fresh waters. — Blackwell. Oxford. 332 pp.

Mundie, J. H., Mounce, D. E. & Smith, L. E. 1973: Observations on the response of zoobenthos to additions of hay, willow leaves, alder leaves and cereal grain to stream substrates. — Fish. Res. Board Can. Tech. Rep. 387.

Murkin, H. R. & Kadlec, J. A. 1986. Responses by benthic macroinvertebrates to prolonged flooding of marsh habitat. — Can. J. Zool. 64:65–72.

Naiman, R. J., Melillo, J. M. & Hobbie, J. M. 1986: Ecosystem alteration of boreal forest streams by beaver (Castor canadensis). — Ecology 67:1254–1269.

Nelson, J. W. & Kadlec, J. A. 1984: A conceptual approach to relating habitat structure and macroinvertebrate production in freshwater wetlands. — Trans. N. Amer. Wildl. Conf. 49:262–270.

Nevers, H. P. 1968: Waterfowl utilization of beaver impoundments in southeastern New Hampshire. — Trans. Northeast Fish & Wildl. Conf. 25:105–120.

Nummi, P. 1984: Waterfowl brood utilization of beaver impoundments. (In Finnish with English summary) — Suomen Riista 31:47–53.

— 1985: The role of invertebrates in the nutrition of dabbling ducks — a review. (In Finnish) — Suomen Riista 32:43–49.

— 1989: Simulated effects of the beaver on vegetation, invertebrates and ducks. — Ann. Zool. Fennici 26:43–52.

— 1990: The differences in the diet of flying juvenile teals and mallards. (In Finnish with English summary) — Suomen Riista 36:89–96.

Patterson, J. H. 1976: The role of environmental heterogeneity in the regulation of duck populations. — J. Wildl. Managem. 40:22–32.

Pehrsson, O. 1979: Feeding behaviour, feeding habitat utilization and feeding efficiency of mallard ducklings as guided by a domestic duck. — Viltrevy 10:193–218.

Pehrsson, O. 1984: Relationships of food to spatial and temporal breeding strategies of mallards in Sweden. — J. Wildl. Managem. 48:322–339.

Pirkola, M. K. & Högmander, J. 1974: The age determination of duck broods in the field. (In Finnish with English summary) — Suomen Riista 25:50–55.

Pöysä, H. 1983: Morphology-mediated niche organization in a guild of dabbling ducks. — Ornis Scand. 14:317–326.

Pöysä, H. & Nummi, P. 1990: Habitat selection of ducks during the breeding season. (In Finnish with English summary) — Suomen Riista 36:97–107.

— 1992: Comparing two methods of data collection in waterfowl habitat use studies. — Bird Study 39, in press.

Reinecke, K. J. & Owen, R. B. 1980: Food use and nutrition of black ducks nesting in Maine. — J. Wildl. Managem. 44:549–558.

Renouf, R. N. 1972: Waterfowl utilization of beaver ponds in New Brunswick. — J. Wildl. Managem. 36:740–744.

Rudqvist, L. 1977: Bäverdammar som andfågelbiotoper. — Inst. Skogszool., Uppsala. 24 pp.

Sjöberg, K. & Danell, K. 1982: Feeding activity of ducks in relation to diel emergence of chironomids. — Can. J. Zool. 60:1383–1387.

— 1983: Changes in the abundance of invertebrates and ducks after flooding of a wetland area in the boreal forest region (N. Sweden). — Proc. Int. Congr. Int. Union Game Biol.: 921–930.

Smirnov, N. N. 1962: Eurycercus lamellatus (O. F. Müller) (Chydoridae, Cladocera): field observations and nutrition. — Hydrobiologia 20:280–294.

Speake, D. W. 1956: Waterfowl use of creeks, beaver swamps, and small impoundments in Lee County, Alabama. — Proc. Ann. Conf. Southeastern Assoc. Game Fish Commiss. 9:1–13.

Street, M. 1977: The food of mallard ducklings in a wet gravel quarry, and its relation to duckling survival. — Wildlfowl 28:113–125.

Sugden, L. G. 1973: Feeding ecology of pintail, gadwall, American wigeon and lesser scaup ducklings in southern Alberta.— Can. Wildl. Serv. Rep. Ser. 24. 43 pp.

Swanson, G. A., Krapu, G. L. & Serie, J. R. 1979. Foods of female dabbling ducks on the breeding grounds. — In: Bookhout, T. A. (ed.), Waterfowl and wetlands — an integrated review: 47–57. Proc. 1977 Symp., Madison, WI, N., Cent. Sect., The Wildl. Soc.

Swanson, G. A. & Meyer, M. I. 1977: Impact of fluctuating water levels on feeding ecology of breeding blue-winged teal. — J. Wildl. Managem. 41:426–433.

Swanson, G. A., Meyer, M. I. & Adomatis, V. A. 1985: Foods consumed by breeding mallards on wetlands of south-central North Dakota. — J. Wildl. Managem. 49:197–203.

Swanson, G. A., Meyer, M. I. & Serie, J. A. 1974: Feeding ecology of breeding blue-winged teals. — J. Wildl. Managem. 38:396–407.

Talent, L. G., Krapu, G. L. & Jarvis, R. L. 1982: Habitat use by mallard broods in south central North Dakota. — J. Wildl. Managem. 46:629–635.

Whitman, W. R. 1976: Impoundments for waterfowl. — Can. Wildl. Serv. Occ. Pap. 22. 22 pp.