Long term stability of boreal lake habitats and use by breeding ducks

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Boreal lake ecosystems are changing due to natural and man-made factors. We studied the long-term stability of the habitat structure in boreal lakes and the habitat use of three duck species: the mallard (*Anas platyrhynchos*), common teal (*Anas crecca*) and common goldeneye (*Bucephala clangula*). The characteristics of the lake habitat were recorded in 1989 and 2009, and duck pairs and broods were surveyed between 1989–1991 and 2007–2009 at 51 lakes in southern Finland. We found some notable lake-specific changes: lakes that had gained more luxuriant vegetation were influenced by humans, while lakes that had lost their luxuriance were small forest lakes. Beaver flooding had caused pronounced alteration to the lakes' habitat structure. Although the habitat features of some lakes had changed, overall, landscape-level lake conditions had not changed. The habitat use of ducks varied between the two time periods in response to regional changes in duck population size and lake-specific habitat changes.

Introduction

Although European boreal lakes can be considered morphologically stable, many anthropogenic processes have affected their trophic conditions. Eutrophication is one of the key processes that has caused striking changes in lake vegetation, and it has also been suggested as an important factor behind changes in the avifauna of boreal lakes since the middle of the 19th century (von Haartman 1973). The nutrient loading of lakes associated with different land uses has been well-studied, but many aspects of the effects of human activity and changes in land use on communities of aquatic species are still poorly known (*see* Hilli *et al*. 2007 and references therein). For example, the study of aquatic vascular plant communities in boreal lakes has mainly focused on species turnover (Virola *et al*. 1999, 2001, Hilli *et al*. 2007), whereas changes in plant community structure and overall vegetation structure have received less attention.

Aquatic plants are considered good indicators of the effects of changes in land use (Hilli *et al*. 2007). The composition of aquatic plant communities also affects duck habitat use and distribution (Nummi and Pöysä 1993, Elmberg *et al*. 1993). Although eutrophication-induced

alterations in aquatic vegetation are often clearly visible (e.g. previously dystrophic lakes have developed eutrophic features), and their effect on long-term changes in waterfowl communities has been recognized (e.g. Kauppinen and Väisänen 1993), studies addressing long-term quantitative changes in both vegetation structure and duck habitat distribution are lacking.

The exploitation of available habitats during the breeding season varies between duck species, and many studies also indicate that habitat requirements and distribution of ducks differ between different phases of the breeding season (Danell and Sjöberg 1978, Pehrsson 1984, Nummi and Pöysä 1993, 1995a, Paasivaara and Pöysä 2008). Consequently, possible long-term changes in habitat use and distribution should be studied separately for pairs and broods. Here we study the long-term stability of habitat structure and the habitat use of three species of duck: the mallard (*Anas platyrhynchos*), common teal (hereafter teal, *Anas crecca*) and common goldeneye (hereafter goldeneye, *Bucephala clangula*). We repeated vegetation descriptions and duck surveys with identical methods on the same lakes studied by Nummi and Pöysä (1993) 20 years ago. We address two main questions: first, whether the habitat structure of the lakes has changed in 20 years; and second, whether the habitat use of duck pairs or broods has changed in 20 years and, in particular, whether such changes could be linked to habitat changes. As habitat use and the distribution of ducks may be density dependent (Fretwell and Lucas 1970, Pöysä 2001), we also consider changes in the population size of the species between the two study periods. Luxuriant vegetation is usually linked to a higher abundance and availability of invertebrates (Voigts 1976, Nummi and Pöysä 1995b), but flooded shores can be an exception, as at the beginning of the inundation emergent vegetation on the shoreline is scarce, but invertebrates are abundant (Nummi 1989). In addition, as some duck species prefer temporally dynamic beaver-flooded ponds as their nesting and, especially, brood rearing habitat (Nummi 1992, Nummi and Pöysä 1997, Nummi and Hahtola 2008), we also accounted for the effects of beaver activity when evaluating changes in habitat structure and duck habitat use.

Material and methods

Study area

The work was conducted in a forested watershed area in Häme, southern Finland (61°12´N, 25°07´E). The area mainly consisted of state-owned hiking land, of which about 10% was lakes and bogs, with the remaining landscape consisting mostly forest. The watershed encompassed 39 km^2 and consisted of 51 lakes and ponds that varied in size (0.1–49.5 ha) and had a total shoreline length of 49.9 km. Every body of water held water for the whole summer and all froze in winter. The forests in the area were typical boreal coniferous forests in commercial use. Forestry was the main human activity in the area. Human settlements were scarce and agriculture was concentrated in small areas of one corner of the study area. The largest human settlement was in the southern part of the area, where the HAMK (University of Applied Sciences) Evo campus (with ca. 300 students) is found, surrounded by three relatively large lakes. The Game and Fisheries Research Station is also situated in the area, and some of the lakes got their water from the station research ponds. For research purposes, one lake in the area had been treated with lime (Rask *et al*. 1996).

Habitat measurements

The habitat measurements included vegetation descriptions and information about the lake structure. The vegetation descriptions were made in July 1989 and 2009. Observer effects were minimal because the same person (PN) supervised and took part both in the vegetation sampling and the duck surveys in both periods.

Shoreline vegetation was described using six vegetation types: (1) forest and bog (i.e. dwarf shrubs or *Sphagnum* formed the shoreline by the lake edge, and there was no emergent vegetation in the water), (2) *Phragmites* on land, (3) *Carex* on land, as well as emergent vegetation in the water (4) *Phragmites*, (5) *Carex,* and (6) *Equisetum*/*Typha*. *Equisetum* and *Typha* shores were combined because they occur in limited shore sections and often together. The width of vegeta-

tion in the water assigned to four classes: (1) 0–1 m, (2) 1–5 m, (3) 5–10 and (4) > 10 m. Similarly, the height of vegetation in the water was also assigned to four classes: (1) 0–25 cm, (2) 25–50 cm, (3) 50–100 cm and (4) > 100 cm. These vegetation types, including width and height classes, were marked on a field map of each lake, and the percentages for the types were calculated from the map data. The coverage of floating leaf vegetation in the lakes was estimated in three classes: (1) 1%–5%, (2) 5%–15% and (3) > 15%. Water depth was measured at a distance of 0.5 m from the shoreline at 5–10 random locations at each lake, with more measurements taken on larger lakes. The lakes were placed in three classes according to their mean depth: (1) 0–50 cm, (2) 50–100 cm and (3) > 100 cm. The depth measurements were recorded at all the lakes in 1989 and were repeated in 2009 only on lakes where flooding conditions caused by beaver activity had changed since 1989, as this could have had a dramatic effect on their depth (Nummi and Hahtola 2008). Thus, for most lakes, we assumed that water depth had changed relatively little over time. The lakes were also placed into four classes according to size: (1) < 0.5 ha, (2) 0.5–2 ha, (3) 2–10 ha and (4) > 10 ha. The same classifications were used in both years.

Duck data

The duck data were collected during the breeding seasons in 1989–1991 and 2007–2009; three successive years were included for both periods to increase the sample size and minimize random variation. Nummi and Pöysä (1993) found that changes in habitat structure were negligible during 1989–1991, the three successive years studied by them, so it was possible to use the habitat data from one year to study duck habitat association with duck data from three successive years. The number of breeding pairs on each lake was estimated on the basis of one pair survey conducted in May of each year. The brood data were gathered with two brood surveys at the beginning of June and July of each year; two additional brood surveys were conducted in late June and July for the years 1990, 1991, 2007 and 2008. Each pair and brood survey included a point survey and

a subsequent round survey in which lakes were circled by foot or by boat; both methods (i.e. the point survey and round survey) are standard duck survey methods in Finland (explained in Koskimies and Väisänen 1991). The age class of each brood was determined using the classification developed by Pirkola and Högmander (1974). Each brood observation was taken into account in order to get a complete picture of habitat use.

Statistical analyses

The 17 habitat variables (Appendix) were analyzed with a principal component analysis (PCA, *see* e.g. Pimental 1979, Gauch 1982), as in Nummi and Pöysä (1993). The PCA was performed upon the correlation matrix. The data from both years (i.e. 1989 and 2009) for all the lakes were included in the same analysis to make the results from both periods comparable for a given lake (*see* also Pöysä 2001). The PCA gave each lake two score values on each component, with the difference between the two lake-specific score values on a given component axis implying change in habitat structure according to that component. The first component explained 23% of the total variation in the habitat data. Score values on the first component are organized in a biologically meaningful gradient. At the positive end, there are large lakes with shallow shores and luxuriant, wide, high vegetation in the water and at the negative end there are small lakes with deep shores and sparse, narrow, and low vegetation (for further details *see* Nummi and Pöysä 1993). Consequently, as in Nummi and Pöysä (1993) and Pöysä (2001), we used the first component as a habitat luxuriance gradient.

We used the lake-specific score values on the habitat luxuriance gradient for two purposes. First, we tracked changes in lake luxuriance and used a paired *t*-test to see if the score values for the two years differed. This test was first applied to all the lakes and afterwards to those lakes which did not show a beaver effect during the research years or the preceding year (e.g. 1988 or 2008) to ensure that the beaver dynamic did not affect the results. Second, for both years we divided the habitat luxuriance gradient into three sections of equal length giving us three habitat

classes (Nummi and Pöysä 1993). This was done in order to check if something had happened in a certain part of the habitat gradient. Lakes at the positive end of the habitat gradient belong to the most luxuriant class, those at the negative end belong to the least luxuriant class; and those in the middle are classed as average. Shoreline length can differ between classes and years. We used the Mann-Whitney *U*-test to test whether the score values for classes or sizes of lakes differed between the years.

The duck data were used in two ways, following, in detail, the approach used in Nummi and Pöysä (1993). First, we used lake-specific presence/absence data for pairs and broods over all three years together with lake-specific habitat luxuriance scores. This produced cumulative data from inhabited lakes over three years, in which one lake could be taken into account three times. To investigate possible changes in duck habitat use between the two study periods, median pair and brood habitat scores between the study periods were compared using the Mann-Whitney *U*-test. Second, using the three habitat classes we compared habitat distribution of pairs and broods between the two study periods. Each of the three habitat classes covered a certain proportion of the total shoreline in the study area. Assuming that the ducks were evenly distributed across the whole study area, these shoreline proportions also indicate expected use of the habitat classes. The duck observations from the lakes for three years were pooled within each habitat class. Therefore, not only the occurrence, but also the number of individuals and broods, of each duck species in each lake was taken into account. The *G*-test was used to see whether the distribution of ducks followed the shoreline proportions of the classes. William's correction was used for teal broods because of small sample size ($n = 13$).

Results

Habitat structure

There was no difference in the lake-specific habitat score values between 1989 and 2009 (1989: $n = 51$, mean $= 0$, SD $= 1.05$; 2009: $n = 51$, mean $= 0$, SD $= 0.95$; two-tailed $t_{50} = 0.05$,

$p = 0.96$). The result was the same when beaver ponds were excluded (1989: $n = 38$, mean $= -0.14$, SD $= 0.95$; 2009: $n = 38$, mean $= -0.15$, SD $= 0.98$; two-tailed $t_{37} = -0.15$, $p = 0.88$). These findings suggest that, at the landscape level, there had been no general unidirectional change in the habitat structure of the lakes.

However, some lakes had undergone large changes over the 20 years, and these changes had been in both directions. No *a priori* threshold exists for distinguishing large changes from negligible changes, so we used the median change of beaver ponds (0.51); 24 out of 51 lakes had changed more than this threshold (Table 1). These lakes can be divided into three classes: beaver-flooded ponds, human-affected lakes and relatively small forest lakes. Among these lakes, natural habitat structure varied widely, as did changes in vegetation. Of the 12 beaver-flooded ponds, 11 were more luxuriant during the flooded year. In beaver ponds that had changed more than the median threshold, the amount of shoreline with *Carex* and *Phragmites* vegetation in the water tended to increase during flooding, and the width of vegetation in the water also increased. Human-affected lakes had become more luxuriant. Two out of three large lakes around the Evo campus had become more luxuriant, as had the lakes downstream of the Game and Fisheries Research Station and the lake treated with lime. The common feature shared by these lakes was their large area. In 2009, the lakes had less shoreline where forest or bog vegetation reached the water's edge, and where there was no emergent vegetation in the water, than was the case in 1989. They also tended to have more shoreline where the shore vegetation consisted of *Carex*, *Phragmites* and *Equisetum*/*Typha* vegetation in the water than was the case in 1989. The width of emergent vegetation in the water had also increased. In contrast, the habitat score values of many small forest lakes had decreased during the 20-year study period. The smaller score values are a result of a decrease in the proportion of *Carex* vegetation in the water, a decrease in floating leaf vegetation, and also a decrease in width of the emergent vegetation in the water. In total, the score values of the larger lakes had shifted in a positive direction on the habitat luxuriance gradient (i.e. they had become more luxuriant), while those of small forest lakes

had shifted in a negative direction (i.e. they had become less luxuriant).

When we tested whether there had been changes in the three habitat classes between 1989 and 2009, we did not find any significant changes in the score values of the lakes (in all cases $p > 0.05$). The amount of shoreline in the three classes was also rather similar in 1989 and 2009 (Fig. 1), and there were no significant changes in the average size of the lakes in the three classes (in all cases $p > 0.05$), even though the mean size of the lakes in the luxuriant class had almost doubled (1989: 12.4 ha and 2009: 21.8 ha).

Distribution of ducks on the habitat structure gradient

The number of lakes used by pairs of ducks (indicated by sample sizes in Table 2) reflected the number of pairs of each species (indicated by

sample sizes in Fig 1) in each of the two study periods; i.e. the number of lakes used increased when population size increased. Nevertheless, there was no connection between the number of used lakes and their average habitat score values; the ducks did not systematically use less luxuriant lakes more when their population increased, or vice versa (*see* Table 2). The habitat distribution of mallard and teal pairs had not changed between the two study periods, whereas goldeneye pairs made greater use of low productivity lakes in 2009, when compared with 1989 (Table 2).

Similarly the number of lakes used reflected the total number of broods (as with pairs above, compare sample sizes in Table 2 and Fig. 1), but again this was not associated with the average habitat score values (Table 2). As with pairs, there was no change in the habitat distribution of mallard and teal broods between 1989 and 2009, but goldeneye broods had shifted towards using less luxuriant lakes (Table 2).

Table. 1. The lakes with the largest changes in habitat score values between 1989–2009 in a descending order. The threshold value for large-scale change is considered to be median change in beaver pond values (0.51). The lakes are classified in three categories with similar lake type/affecting factors. For beaver ponds the year of flooding is also given.

| Lake	Score values		Change	Lake type/ affecting factor
	Year 1989	Year 2009		
Kärppijärvi	−1.12	1.03	2.15	Beaver 2009
Alinen rautjärvi	0.60	1.42	0.82	Human affected
Pitkänniemenjärvi	−0.63	0.17	0.80	Human affected
Majajärvi	0.07	0.80	0.73	Forest lake
Tervajärvi	−1.20	−0.50	0.70	Beaver 2009
Pitkännimenjärven lammi	−0.79	−0.10	0.68	Human affected
Keskinen Rautjärvi	0.91	1.51	0.60	Human affected
Valkjärven rimpi	−1.85	−1.25	0.60	Human affected?
Syrjänalusen rimpi	0.52	1.08	0.56	Forest pond
Iso Valkjärvi	−1.45	−0.94	0.51	Human affected
Vähä Vehkajärvi	1.75	1.24	−0.51	Beaver 1989
Hautjärvi	1.08	0.57	−0.52	Forest lake
Iso Ruuhijärvi	0.44	−0.08	−0.52	Beaver 1989
Lapinjärvi	0.40	−0.15	−0.55	Forest lake
Alinen Mustajärvi	−0.61	−1.19	−0.58	Forest lake
Keskinen Mustajärvi	0.56	−0.05	−0.61	Forest lake
Karvalammi	0.60	−0.02	−0.62	Forest lake
Tekumi	1.30	0.65	−0.66	Beaver 1989
Vähä Ruuhijärvi	0.58	−0.08	−0.66	Forest lake
Häntjärvi	0.56	−0.18	−0.74	Beaver 1989
Viitajärvi	0.21	−0.58	−0.79	Forest lake
Ylinen Mustajärvi	0.65	−0.25	−0.90	Forest lake
Tohijärvi	1.83	0.92	−0.91	Beaver 1989
Likojärvi	1.46	0.31	−1.15	Forest lake
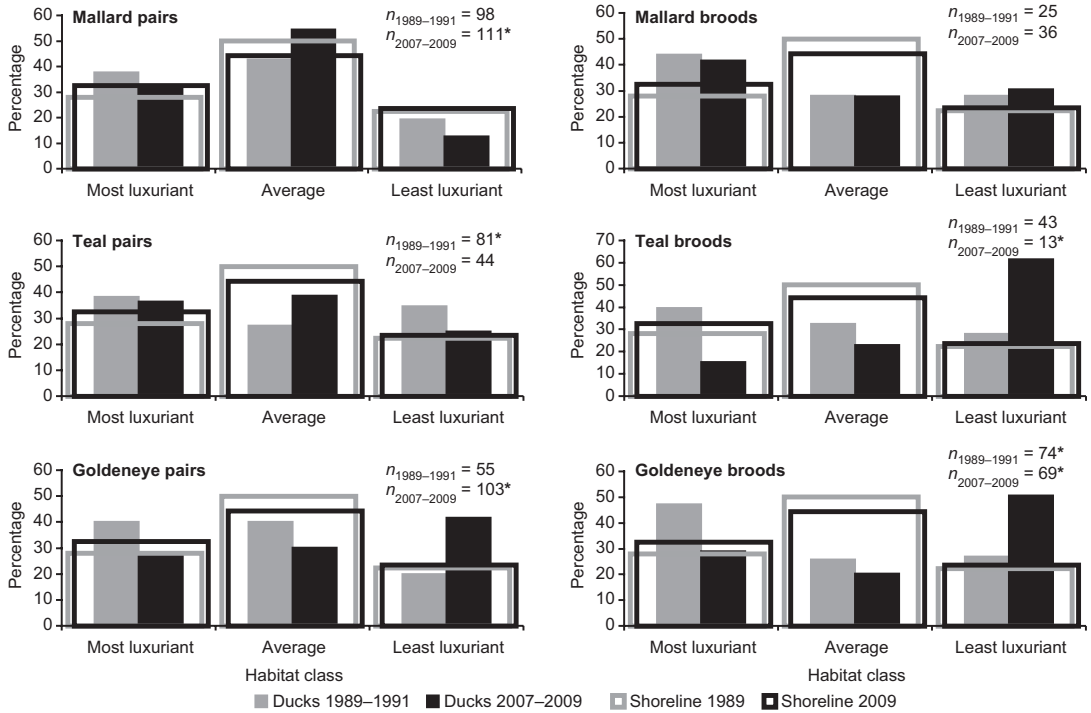
Fig. 1. Use of the three habitat classes by mallard, teal and goldeneye pairs and broods. The bars represent observed habitat use and the lines represent expected use of each habitat class (i.e. the proportion of shoreline of the lakes within a given habitat class of the total shore line of all lakes). n = the total number of pairs and broods in the study periods. The asterisks indicate that observed habitat use differs significantly ($p < 0.05$) from expected habitat use (*see* text).

Use of habitat classes

There was no systematic change in the use of the three habitat classes by the duck species between the two study periods, other than that the use of the most luxuriant habitat class had tended to decrease from 1989 to 2009 for both pairs and broods of all species; the variation, however, was large (Fig. 1).

The number of pairs and broods of mallard was very similar in both study periods, as were the patterns of habitat use. For mallard pairs,

Table 2. The median habitat score values of lakes used by mallard, teal and goldeneye pairs and broods in 1989–1991 and 2007–2009. Mann-Whitney *U*-test is two-tailed. n = the cumulative number of lakes used during the three years. The asterisks indicate significant differences.

	Period	n	Median	Mann-Whitney U	p
Mallard pairs	1989–1991	55	0.44	1518	0.66
	2007–2009	58	0.49		
Teal pairs	1989–1991	53	0.07	734	0.42
	2007–2009	31	0.34		
Goldeneye pairs	1989–1991	38	0.58	764	0.02*
	2007–2009	57	−0.15		
Mallard broods	1989–1991	14	0.90	166	0.65
	2007–2009	26	0.75		
Teal broods	1989–1991	24	0.58	67	0.10
	2007–2009	9	−0.50		
Goldeneye broods	1989–1991	30	0.60	274	0.02*
	2007–2009	28	−0.11		

the use of the three habitat classes differed from expected use in the second period ($n = 111$, two-tailed $G = 8.93$, $p = 0.01$; Fig. 1). The size of the teal population collapsed in the second study period. The habitat use of teal pairs showed the same pattern as that of mallard pairs, but it differed from expected use in the first period ($n = 81$, two-tailed $G = 17.62$, $p = 0.0001$; Fig. 1). Teal broods used less luxuriant lakes more than expected in the second period ($n = 13$, two-tailed $G = 8.18$, $p = 0.02$; Fig. 1). The number of goldeneye pairs almost doubled in the second study period, but the number of broods did not change. Nevertheless, both pairs and broods used less luxuriant lakes more than expected in the second period. In particular, the habitat use of goldeneye broods differed between the study periods: in the first period they preferred the most luxuriant habitat class, whereas, in the second period, the least luxuriant habitat class was preferred (1989–1991: broods; $n = 74$, two-tailed $G = 19.53$, $p < 0.0001$; 2007–2009: pairs: $n = 103$, two-tailed $G = 17.84$, $p = 0.0001$; broods: $n = 69$, two-tailed $G = 27.93$, $p < 0.0001$; Fig. 1).

Discussion

Habitat change

The habitat structure of the lakes at the landscape level had not changed systematically between 1989 and 2009. A closer examination, however, revealed some notable changes in individual lakes. The beaver effect was strong in some lakes. The effect was not systematic, but it was dynamic both spatially and temporally. We also found systematic changes operating in opposite directions. Similarly, Hilli *et al.* (2007) found that changes in land use could have both a negative or positive effect on diversity and the abundance of aquatic plants. In our study, the lakes that had become more luxuriant were near human settlements or were influenced by humans in other ways (e.g. treated with lime). It seems that human settlements increase diffuse nutrient loading (Meriläinen *et al.* 2000) and affect lakes locally. These lakes also tend to be the largest lakes in the area.

The lakes that had lost their luxuriance in terms of habitat structure were usually small lakes surrounded by forest. This may be a normal succession, but we do not know the factors driving the changes. In the study area used by Hilli *et al.* (2007), all the small lakes lost water and their area diminished, and the authors suggested that this led to the disappearance of some aquatic vascular plant species. Unfortunately, we do not have data on water levels, but most of the forest lakes in our study had stable habitat score values. Only one forest lake and one shallow pond had become more luxuriant without the influence of man or beavers. We did not study changes in land use within the study area. Hilli *et al.* (2007) found that the effect of land use on the turnover of aquatic vascular plant species is weak at distances more than 100 m from a lake. Within our study area, coniferous forest dominated the surroundings of the lakes, and the main type of land use was forestry. Forestry, which is an important type of land use in Finland, may change the trophic status of lakes and so influence the biota (Winkler *et al.* 2009); however, its implications are poorly known. Even though we did not specifically study the impact of forestry, our results suggest that it had not caused habitat changes in the lakes, at least not during the 20-year study-period. On the other hand, if the impact of forestry on water quality is only short term (Winkler *et al.* 2009), we may not have detected its effect on habitat in the time scale of the present study. In general, the forest lakes in our study area had a stable habitat structure; if some directional changes had taken place, it was that the lakes may have become slightly less luxuriant.

In conclusion, for the area as a whole, the mean and deviation for the lake-specific habitat scores remained about the same between 1989 and 2009. However, some changes in both directions had occurred, and it is possible that this deviation will increase in the future because some lakes had lost their luxurance and others, especially the largest ones, had become more luxuriant.

Habitat use

Because the habitat structure of the lakes proved to be stable at the landscape level, we did not expect drastic changes in the habitat distribution

of ducks. On the other hand, when changes in habitat distribution were observed, some other factors, such as changes in population size or local lake-specific changes in habitat structure, may have been involved. Of the three species studied, the habitat use and population size of the mallard remained unchanged between the two study periods. In contrast, the other two species, teal and goldeneye, showed clear changes in both habitat use and population size.

The habitat use of teal broods had shifted in a less luxuriant direction, and they used the least luxuriant class of lakes clearly more than expected in 2007–2009. The number of teal pairs and broods had decreased dramatically from the first period to the second, and annual numbers of teal have recently been very low. This meant that even one pair or brood had a large impact on the results, but it also meant that teal could quite freely choose their lakes. Both teal pairs and broods prefer beaver-flooded lakes and ponds (Nummi and Pöysä 1995a, 1997, Nummi and Hahtola 2008), and they also thrive in small wetlands (Nummi and Pöysä 1995b). In the second period of the present study, the majority of teal broods were seen in a single beaver pond (Huhmari). Because the success of teal broods was found to be better in beaver ponds than in the other bodies of water in the study area (Nummi and Hahtola 2008), we can assume that the habitat distribution of teal broods reflects ideal free habitat selection (*see* Fretwell and Lucas 1970, Pöysä 2001).

The lakes occupied by goldeneye pairs and broods were less luxuriant in 2007–2009 than in 1989–1991. The same pattern was seen in the use of habitat classes: in 1989–1991 goldeneye pairs and broods used the luxuriant class more than expected, whereas in 2007–2009 the use of the luxuriant class dropped to just below the expected level, and the use of the least luxuriant class increased to above the expected level. Although, goldeneye seems to favor luxuriant lakes, other factors also determine their habitat distribution. Based on our original data (Suhonen 2011) it seems that goldeneye prefers beaver ponds irrespective of their luxuriance, and this may explain the goldeneye's increased use of the least luxuriant class in 2007–2009. In 1989–1991, most of the flooded ponds were

in the luxuriant class, but in 2007–2009 the proportion of flooded ponds in the average and least luxuriant classes was higher. The actual number of flooded ponds dropped slightly in the second study period. In particular, one beaver pond (Huhmari) in the least luxuriant class in 2007–2009 was actively used by goldeneye pairs and broods. As the goldeneye is a territorial species (Eadie *et al.* 1995, Ruusila and Pöysä 1998), it seems odd that goldeneye densities in small beaver ponds can become so high. One possibility is that because of the rich structure of beaver ponds (i.e. rich vegetation, plenty of dead trees and bushes, small islands) ducks can more easily avoid visual contact, and therefore densities can rise.

As indicated by the total number of pairs in the two study periods (*see* Fig. 1), the goldeneye population had grown during the 20-years study period. Due to territoriality, goldeneye pairs had been forced to spread to unoccupied lakes. Here it should be noted that all the lakes included in the present study had nest boxes for goldeneyes (*see* Paasivaara and Pöysä 2008). In the second study period, there were just seven lakes in the luxuriant class, but the two other classes had about 20 lakes each. Hence, the two less luxuriant classes had more potential territories, and when the population grew, the goldeneye spread to these lakes. The habitat use of goldeneye pairs differed from expected use in the second period, and the habitat use of goldeneye broods differed from expected use in both periods. In the first period, goldeneye pairs were quite evenly distributed throughout the area, although slightly preferring luxuriant lakes and beaver ponds. When the beaver ponds shifted in a less luxuriant direction and population size increased the habitat use of goldeneye pairs also shifted to less luxuriant direction. Goldeneye broods are even more strongly associated with beaver ponds, (Nummi and Pöysä 1995a) and they track the spatial and temporal dynamics of beaver ponds in the area. As the number of goldeneye broods had not increased from the first period to the second, it is possible that the goldeneye has reached the upper limit of production in the area (*see* also Pöysä and Pöysä 2002).

Our findings on the habitat use of teal and goldeneye emphasize that in barren boreal areas

like Evo even one really good pond can be of central importance to ducks. Beavers can make barren lakes suitable for ducks and so drive ducks' habitat use. In the Evo area this might become more important in the future because if forest lakes continue to lose their luxuriance, more and more lakes would become unsuitable for ducks.

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Appendix. Habitat variables and values in the first component.

Habitat variable	The first component
Forest and bog	−0.289
Phragmites on land	−0.337
Carex on land	−0.557
Phragmites in the water	0.525
Carex in the water	0.257
Equisetum/Typha in the water	0.499
Width 1	−0.899
Width 2	0.700
Width 3	0.540
Width 4	0.427
Height 1	−0.271
Height 2	−0.161
Height 3	0.042
Height 4	0.293
Floating leaf	0.427
Depth	−0.740
Size	0.474