

# Mortality of common goldeneye (*Bucephala clangula*) broods in relation to predation risk by northern pike (*Esox lucius*)

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We studied brood-rearing lake selection of the common goldeneye *Bucephala clangula* in relation to food abundance, vegetation structure, brood mortality and predation risk by northern pike *Esox lucius*. Movements of radio-tagged females and their broods were followed and duckling survival was determined until fledging or until the young had died. Food was more abundant in rearing lakes than in reference lakes. On the contrary, no difference was found between rearing and reference lakes with respect to the structure of shore vegetation. During the brood rearing period the mortality of young (1–23 days) ducklings increased with the increased predation risk by pike. Mortality of old (> 23 days) ducklings was not associated with the predation risk by pike. These results suggest that pike predation is an important source of mortality in young common goldeneye ducklings, and that females may be imperfect in predicting pike predation risk when selecting the brood rearing lake.

## Introduction

During the process of habitat selection individuals make choices based on cues that correlate with habitat quality (Hildén 1965, Cody 1985, Storch 1993). This is especially important in the selection of breeding habitat, where food should play a central role, because individuals should gain sufficient energy to survive and reproduce. Predation risk should also influence habitat selection since predation can increase adult mortality and decrease productivity (Newton 1998). If predation risk is associated with foraging, individuals have to adjust

their behaviour to trade-off food acquisition for predator avoidance (Fraser & Huntingford 1986, Sih 1987, Lima & Dill 1990). Thus, predation may modify habitat selection based on resource availability as shown e.g. in little blue herons, *Egretta caerulea* (Caldwell 1986). However, the relationship between these trade-off components may be complex. Under certain circumstances, individuals may make poor choices by relying on cues that correctly reflect current levels of critical resources like food, but are not reliable in predicting predation risk. This phenomenon may occur if the environment changes suddenly, and hence, the prevailing habitat selection behaviour

may not correlate with the expected reproductive outcome (Levins 1968). Alternatively, insufficient antipredatory responses of individuals may reflect constraints imposed by unpredictable predation (Dwernydchuk & Boak 1972, Lima & Dill 1990, Pasitschniak-Arts & Messier 1995).

The common goldeneye *Bucephala clangula* is a long-lived hole-nesting precocial duck with self-feeding young. After nest exodus, which takes place within 48 hours of hatching, broods typically use one or several patches (wetlands) during the brood-rearing period. Previous studies have shown that food abundance is an important factor in habitat selection of common goldeneye broods (Eriksson 1978, 1979a, Eadie & Keast 1982, Pöysä & Virtanen 1994, Wayland & McNicol 1994), but also habitat structure, indicating cover from predators and productivity of the patch, may influence the habitat selection of broods (Nummi & Pöysä 1993, 1995a, 1995b). It has been suggested that resource shortage may initiate between lake movements if the current lake does not fulfill the food requirements of a brood (Sirén 1952, Eriksson 1978, 1979a, 1979b, Eadie & Keast 1982, Pöysä & Virtanen 1994, Wayland & McNicol 1994). In addition, Sjöberg *et al.* (2000) demonstrated that many boreal lakes are suboptimal duckling habitats and food limitation may be a general phenomenon in these environments. Earlier studies have also found much variation in the survival of common goldeneye broods (Pöysä 1992, Pöysä & Virtanen 1994, Wayland & McNicol 1994, Pöysä *et al.* 1997, Milonoff *et al.* 1995, 1998), but environmental or habitat factors explaining brood survival have proved difficult to identify. However, Wayland and McNicol (1994) found that brood survival was higher in clustered lakes than in isolated lakes, the former probably enabling broods to be better able to avoid predators, competitors and food shortage. Nevertheless, predation appears to be a serious threat in young ducklings of many species of ducks. The high rates of duckling mortality reported in earlier studies underscore the need to identify and evaluate the magnitude and sources of mortality during brood-stage habitat selection (e.g., Rotella & Ratti 1992, Dzus & Clark 1997, Krapu *et al.* 2000, Nummi & Pöysä 1995a, Ringelman & Longore 1982, Guyn & Clark 1999, Savard *et*

*al.* 1991, Savard *et al.* 1991, Dawson & Clark 1996).

In northern Europe, breeding lakes of ducks are stable and they hold abundant fish populations, which may have a complex influence on water bird populations (Eriksson 1983, McNicol *et al.* 1987). Abundant prey populations frequently uphold populations of large predatory species such as the northern pike *Esox lucius*, which is a common top predator occupying almost all stable freshwaters in northern Europe (Maitland & Campbell 1992). Feeding habits of the adult pikes are versatile: they eat a wide range of fish species (e.g., Frost 1954, Maitland & Campbell 1992), but also small mammals and ducklings of different waterfowl species (Bajkov & Shortt 1939, Solman 1945, Lagler 1956, Maitland & Campbell 1992). The coexistence of pike and ducklings is inevitable when females of goldeneyes and other duck species use meso-eutrophic wetlands for brood rearing. Nevertheless, predation pressure from the pike has not been considered important in lake selection of common goldeneye broods (Eriksson 1978, Beattie & Nudds 1989) even though predation by pike has been identified as a cause of death of small ducklings (Solman 1945, Lagler 1956, Eadie *et al.* 1995). However, the relationship between the survival of common goldeneye ducklings and mortality risk by pike has not been studied before.

This paper has two aims. First, based on data from radio-tagged females with broods, we study habitat selection of common goldeneye broods in relation to food abundance and vegetation structure, which are the most apparent factors affecting the habitat-selection decisions in the species. Second, we explore whether the mortality of different-aged broods in a particular rearing site is related to predation risk by the pike.

## Material and methods

### Study area

The 75 km<sup>2</sup> study area is a barren forested watershed area surrounding the Evo Game Research Station in Lammi, southern Finland (61°13'N, 26°06'E; *see* Rask & Metsälä 1991). The area

is dominated by pine *Pinus sylvestris* or mixed (pine, birch *Betula* spp. and spruce *Picea abies*) forests, inter-dispersed with small lakes (0.04 to 49.5 ha) that comprise about 7% of the total area (see Fig. 1). The lakes are situated at between 125–155 m above sea level, and their shore type vary from oligotrophic bog and forest without emergent plants to more eutrophic ones with lush stands of *Equisetum* and *Typha* (Rask & Metsälä 1991). There were 100–150 artificial nest boxes available for common goldeneye in the study area between 1989–2001. At least one nest box was available at each lake.

### Marking of females, lake selection and survival of broods

Common goldeneye females were marked with radio transmitters and wing tags during the breeding seasons of 1989–2001. Females were captured usually 1–2 days before or a few hours after hatching. Mean hatching date in our study population was 9 June (range 17 May–28 June, 133 nests). Females were marked with two-stage radio transmitters (TW-2 from Biotrack), which were attached at the proximal ends of tails (see picture by Giroux *et al.* 1990). All females were also fitted with plastic colored wing tags on one or both wings (modified from the method of Anderson 1963) and individually marked steel or aluminum leg rings. Pöysä and Virtanen (1994) give more information on catching and marking of females.

Altogether 98 females were individually marked with radio transmitters and wing tags. In addition, we marked six females only with wing tags and steel leg rings. Females and broods were relocated at varying intervals (mean 2.3 days, SD = 2.1,  $n = 1\ 263$  intervals) after the brood left the nest box, and during each relocation brood size was determined. Movements of marked females and their broods and duckling survival were determined until fledging age (approximately 60 days of age) or until the young had died. Because brood mortality was high soon after nest exodus, sudden total-brood losses were common and we lost the contact with some females for a while or permanently. The monitoring period per brood varied considerably, i.e. from 1 to 67 days (mean

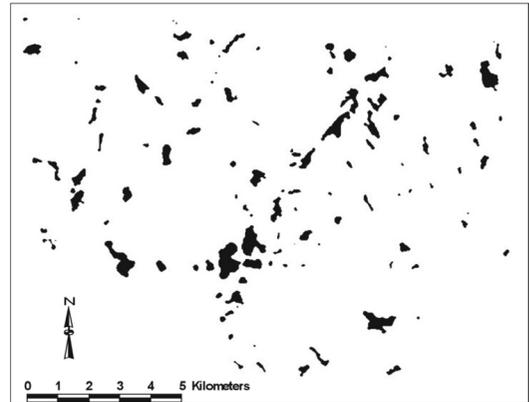


Fig. 1. Map of the study area showing the distribution of permanent small lakes and ponds (black polygons) surrounded by forests (white area). Rivers and ditches are not shown.

28.6 days, SD = 21.5,  $n = 104$  monitoring periods).

To study lake selection by broods, we used brood relocations and identified the lakes used by each brood (note that, hereafter, lake or habitat selection by broods refers to selection by the female attending the given brood). These lakes were divided into two categories that are referred to as reference lakes and rearing lakes. Reference lakes were used only temporarily, even if the brood had the opportunity to stay there. Rearing lakes include one or several lakes consistently used by the brood during the whole monitoring period. Hatching lake may classify to reference or rearing lake depending on the occurrence of the brood on that lake.

Using data from brood relocations, we calculated two mortality rates, i.e. brood-specific daily mortality rate and lake-specific daily mortality rate, according to Ringelman and Loncore (1982; see also Gauthier 1987; a method applied from Mayfield 1961, 1975). This method takes into account both the brood size and the duration of the period over which the mortality is calculated. Note that the brood-specific mortality also includes mortality during brood movements between lakes. Because predation risk by pike is a feature of a given lake, the brood mortality data were examined in more detail. To get an accurate rearing lake-specific (brood) mortality, we used only brood relocations that fulfilled the following two requirements: first, the brood had

to stay in the rearing lake between successive relocations and, second, if mortality occurred, we had to be sure that it took place in the same rearing lake in a given monitoring period. Using these criteria, we had 46 broods in 19 different rearing lakes for which we managed to calculate the rearing lake-specific mortality. Each year between 1989–2001 contributed to these brood data (mean 3.5 broods per year, SD = 1.7, range 2–7; mean brood size at nest exodus 7.9, SD = 1.1, range 5–13). The rearing lake-specific monitoring periods varied from one to 65 days (mean = 27.1, SD = 18.5,  $n = 58$  monitoring periods). To calculate the rearing lake-specific daily mortality rate for each lake, means of these separate monitoring periods were used. Because we monitored survival of broods until fledging age and predation by pike may affect young and old ducklings differently (*see* Milonoff *et al.* 1995), we calculated rearing lake-specific daily mortality rate separately to the two age categories: age-class I (1–23-day-old ducklings), age-class II and older (> 23-day-old ducklings), respectively (Pirkola & Högmänder 1974).

### Environmental variables

To assess factors that may affect habitat selection of goldeneye broods, we measured food resources and vegetation structure of the lakes used by the broods. Food resources of the lakes were estimated with activity traps (*see* fig. 1 in Murkin *et al.* 1983) that were identical with the traps used by Elmerberg *et al.* (1992). Trapping was done in the breeding seasons 1990–1995 between 11 July and 3 August. Pöysä and Virtanen (1994), and Nummi and Pöysä (1993, 1995a, 1995b) give more information on sampling and analysis procedure of invertebrate data. In brief, ten traps were used per lake. Five traps were in the most luxuriant section (regarded as ‘best’ foraging area) of the shoreline and the other five traps were placed in a typical section. In lakes with homogenous shoreline, all ten traps were placed in a single area. Because the proportions of shore types varied between lakes, results from the two trapping sites were weighted in proportion to their occurrence along the total shore of a given lake. The traps were set parallel to the shore, 1 m

from the shoreline where the water depth ranged from 25–75 cm. The distance between traps was 3 m and traps were left for 48 hours. Trap content was poured into a sieve (mesh size 1 mm), bottled and identified in the laboratory. The length of all individuals was measured and assigned to six length categories (Nudds & Bowlby 1984). Zooplankton (*Cladocera*) were excluded since they are not important prey for goldeneye ducklings (Eriksson 1976, 1978). As in Elmerberg *et al.* (1992) and Pöysä and Virtanen (1994), an index of food abundance was calculated by multiplying the number of individuals in each prey taxon by its mean length. The final index of food abundance of a lake is thus the total number of individuals per one trap and one trapping day weighted by the size classes of invertebrates and the proportion of the two shore line types.

Structure of vegetation in the lakes in our study area was mapped in late July 1990. Details of variables used in this study are given in Pöysä and Nummi (1992). In brief, 18 different variables were measured to describe the structure of shore vegetation in the lakes. A principal component analysis (PCA, Pimental 1979) was used to arrange the lakes on gradient based on the correlation matrix of the 18 variables. First axis (PC1) explained 27% of the variance and represented a biologically sound habitat gradient, i.e. from the lakes with barren shore vegetation (negative end of the PC1) to those with luxuriant shore vegetation (positive end of PC1). The component scores of the lakes on the gradient were used as an index of vegetation structure of the lakes (Pöysä & Virtanen 1994).

We made a comparison between the reference lakes and rearing lakes for each brood with respect to the index of food abundance and the index of vegetation structure. If more than one lake was included in either category, we calculated means from the lakes and used the mean values in the comparisons. In these analyses, we used data from the 46 broods for which we were able to calculate the rearing lake-specific mortality (*see* above). All the variables mentioned above were not available for all lakes and broods, and, therefore, sample sizes vary between analyses.

Because the data for the environmental variables were not available from all the years from

which the brood data were, it is important to assess the constancy of food resources and vegetation structure of the lakes across years. Also, within-season constancy of food resources may be of concern since lake selection by common goldeneye broods takes place in June, while the food resource data are from July–August. Using data from eight lakes and 12 years (1989–2000), we have shown that the abundance of nektonic invertebrates varies considerably between the lakes and there is a high concordance in the rank of the lakes among years (*see* Fig. 1, food index 2, and associated test statistics in Elmberg *et al.* 2003; *see* also Pöysä *et al.* 2000: p. 583). Similarly, using data from 12 lakes and four trapping periods (i.e. 8–15 May, 15–28 May, 7–18 June, and 3–17 July) in 1990, we have shown that there is a high concordance in the rank of the lakes among the trapping periods (within season) in terms of the abundance of nektonic invertebrates (Pöysä *et al.* 2000: p. 585, Pöysä & Virtanen 1994: p. 292). Repeatability (Lessells & Boag 1987, Krebs 1999) of the food indices between years was  $r = 0.237$  ( $F_{7,88} = 4.721$ ,  $p < 0.001$ ), and that within-seasons was  $r = 0.333$  ( $F_{11,36} = 3.000$ ,  $p = 0.006$ ). As mentioned in Nummi and Pöysä (1993: p. 320), vegetation structure of the lakes in the present study area was mapped and analysed each year between 1988 and 1990. We used the yearly component scores (PC1) of the lakes (51 lakes) and, as with the food indices, calculated Kendall's coefficient of concordance and repeatability of the lake scores across years. Kendall's coefficient of concordance ( $W$ ) was 0.856 ( $\chi^2_{50} = 128.4$ ,  $p < 0.001$ ) and repeatability was 0.819 ( $F_{50,102} = 14.337$ ,  $p < 0.001$ ). We conclude that, considering the relatively high concordance and repeatability of the environmental variables, they are constant and reliable enough to index the status of each lake over longer time scales (*see* also Pöysä & Virtanen 1994, Pöysä *et al.* 2000, Elmberg *et al.* 2003).

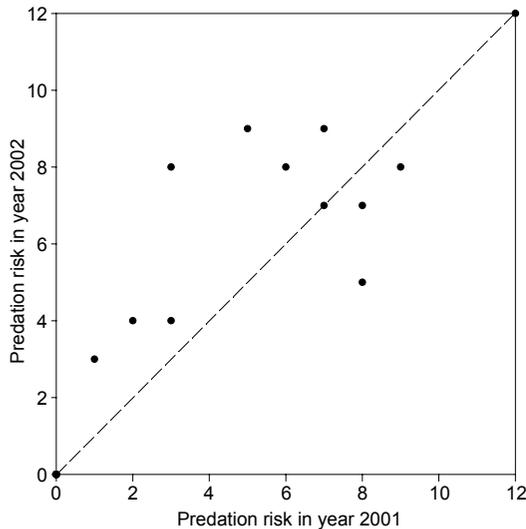
### Lake-specific predation risk by pike

Lake-specific pike predation risk (i.e. the relative threat of an attack) may consist of at least two main factors, the abundance (or density) and feeding behaviour of pike in the lake. Hooking is

a selective method of sampling predatory fishes and it can be used also to indicate true predatory behaviour and feeding activity of predatory fishes such as the pike. Furthermore, hooks can be used effectively in varying depth and vegetation conditions (Maitland & Campbell 1992). In this study, we used special hooks for pike, i.e. bait hooks, which are 12.5 centimeters long, made of brass and provided with a baitfish. For a baitfish, we used small (8–13 cm) roach *Rutilus rutilus* and perch *Perca fluviatilis* exclusively, which are the main food sources of pike in our study area (Raitaniemi 1995). Baitfishes were obtained by netting and killed immediately before hooking. These special bait hooks are commonly used in recreational pike fishing in Fennoscandia.

To get a lake-specific index of pike predation risk in the rearing lakes we sampled pike with bait hooks in the first half of July 2001 and 2002. Four bait hooks per lake were placed in the mid-water parallel to and about 1 m from the shoreline or to the zone between emergent vegetation and free water where the depth of water ranged between 20–100 cm. This placement of hooks is relevant because pike tend to inhabit the shallowest parts of lakes (Casselman & Lewis 1996). All four hooks were placed in a single randomly selected area and the distance between the hooks was 10–15 m. Hooks were left for three days (72 h) in each lake. Captured pikes were killed and preserved for further investigation in the Evo State Fisheries and Aquaculture Research Station. Because most of the pike tended to be lost during angling (i.e. the hook came off), an index of predation risk in each year was measured as a total number of attacks per lake instead of caught fishes. Although there was a strong correlation between the number of the attacks and number of the caught pike per lake in both years (2001:  $r_s = 0.807$ ,  $n = 19$ ,  $p < 0.001$ ; 2002:  $r_s = 0.719$ ,  $n = 19$ ,  $p < 0.001$ ), the total number of attacks per lake is likely to indicate more reliably true predation activity of pike in a given lake.

We repeated the same sampling procedure in 2001 and 2002 to find out if the index of lake-specific predation risk was constant between years. This was crucial since the brood mortality data were collected before fish sampling. There was a strong correlation in the number of lake-specific attacks between years ( $r_s = 0.885$ ,  $n =$



**Fig. 2.** The constancy of the index of lake-specific predation risk by pike between 2001 and 2002. The data are based on a repeated sampling procedure during successive years in the same lakes ( $n = 19$ ; the index was zero for seven lakes in both 2001 and 2002; see Material and methods, Lake-specific predation risk by pike). The dashed diagonal line indicates equal index values of the lake-specific predation risk in the two years.

19,  $p < 0.001$ ; Fig. 2), and the repeatability of pike predation risk was high ( $r = 0.884$ ,  $F_{18,19} = 16.226$ ,  $p < 0.001$ ). This means that predation risk by pike was relatively constant between years in a given lake. We used the mean number of attacks per year as an index of predation risk by pike for each rearing lake.

Normality of all variables was tested with the Lilliefors test. Because most of the variables did not meet the requirements of parametric tests even after transformations, we used nonparametric tests throughout. All significance levels are for two-tailed tests.

## Results

### Lake selection of broods

Most (35 out of 46) broods left the hatching lake during the first two days. Before a brood settled down after the nest exodus, it rejected on average 2.8 lakes (Range = 1–7;  $n = 35$ ). A given brood used, on average, 1.6 lakes as rearing lakes (range

= 1–5;  $n = 46$ ), and 17 of the 46 broods changed the rearing lake during the rearing period. Food was more abundant in rearing lakes than in reference lakes (Table 1), but no differences were found between the reference and the rearing lakes with respect to the index of vegetation structure (Table 1). There was no correlation between the index of food abundance and the index of vegetation structure ( $r_s = -0.03$ ,  $n = 24$ ,  $p = 0.881$ ).

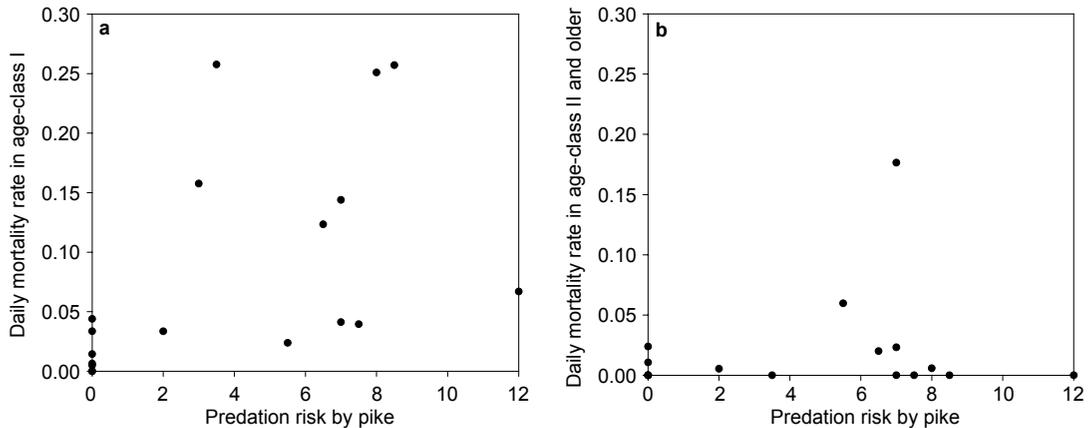
### Brood mortality in relation to predation risk by pike

Duckling loss was high since 8 broods of 46 were totally destroyed and 47.4% of the survived broods ( $n = 38$ ) lost more than half of the ducklings. Daily mortality rate of ducklings during the whole rearing period varied considerably between the broods, from 0 to 0.743 (mean = 0.086,  $n = 46$ ; 95% confidence limits for the mean: lower = 0.050, upper = 0.129; confidence limits calculated on the basis of 10 000 bootstrap samples of the original data). Daily mortality rate of ducklings in the broods of age-class I was higher than in the broods of age-class II or older (Table 2, brood-specific mortality). Similarly, the lake-specific mortality rate varied between the age classes (Table 2, lake-specific mortality).

Lake-specific mortality rate of ducklings in the age-class I increased with the lake-specific index of pike predation risk ( $r_s = 0.691$ ,  $n = 18$ ,  $p = 0.002$ ; Fig. 3a), whereas no correlation was found between the lake-specific index of pike predation risk and the lake-specific mortality rate of ducklings in age-class II or older ( $r_s = 0.010$ ,  $n = 17$ ,  $p = 0.971$ ; Fig. 3b).

## Discussion

Our findings based on a large set of individually known broods confirm the observations of previous studies that common goldeneye broods select lakes other than the nesting lake for rearing (Pöysä & Virtanen 1994, Wayland & McNicol 1994). Desertion of hatching lake seems to be a rule, at least within a rather dense network of small lakes as was the case in our study. As expected, food abundance played an important



**Fig. 3.** Lake-specific daily mortality rate of (a) age-class I broods (1–23-day-old ducklings) and (b) age-class II and older broods (> 23-day-old ducklings) in relation to lake-specific predation risk by pike.  $n = 18$  lakes in panel a (two data points overlap at  $x = 0, y = 0$ ) and  $n = 17$  lakes in panel b (four data points overlap at  $x = 0, y = 0$ ).

role in lake selection by the broods (*see* also Eriksson 1978, 1979a, Eadie & Keast 1982, Pöysä & Virtanen 1994, Pöysä *et al.* 1994, Wayland & McNicol 1994). Even though food was more abundant in the rearing lakes than in the reference lakes, some of the food-rich lakes were rejected by the broods, implying that other factors also influenced the lake preference of the broods. However, vegetation structure did not appear an important factor in the present study. Similarly,

in a study based on census data, Nummi and Pöysä (1993) did not find an association between common goldeneye brood density and habitat luxuriance, and brood density increased only with the abundance of nektonic invertebrates. The lack of association with vegetation structure may reflect the open feeding habits of common goldeneye ducklings (Eriksson 1976, Nummi & Pöysä 1995b). Moreover, vegetation structure and food abundance seemed to be independent

**Table 1.** Quartiles (25th, 50th, 75th) of environmental variables in reference and rearing lakes of the common goldeneye broods. Difference between reference and rearing lakes were tested with Wilcoxon's signed rank test.  $n$  gives the number of broods (females).

	Reference lakes			Rearing lakes			$Z$	$p$	$n$
	25th	50th	75th	25th	50th	75th			
Food abundance index	7.50	9.40	21.15	12.33	31.94	42.97	-3.01	0.003	26
Structure of vegetation	-0.35	-0.10	0.80	-1.83	0.30	1.40	-0.15	0.881	20

**Table 2.** Quartiles (25th, 50th, 75th) of brood-specific and lake-specific daily mortality rate of the common goldeneye broods. Note that brood-specific mortality also includes mortality occurring during brood movements between lakes, whereas lake-specific mortality only includes mortality occurring within the rearing lakes. Differences of brood-specific and lake-specific daily mortality rates between age-class I and age-class II or older were tested with Wilcoxon's signed rank test.  $n$  gives the number of broods or lakes, as appropriate.

	Age-class I			Age-class II or older			$Z$	$p$	$n$
	25th	50th	75th	25th	50th	75th			
Brood-specific	0.014	0.025	0.055	0.000	0.008	0.033	-2.57	0.010	35
Lake-specific	0.016	0.025	0.050	0.000	0.009	0.031	-2.33	0.020	16

lake characteristics in our study area (*see also* Nummi & Pöysä 1993). Pöysä and Virtanen (1994) found that lake water chemistry (mainly acidity) and size were important factors in the lake selection of common goldeneye broods. However, these characteristics were not important on their own but their association with lake selection was evidently due to food resources (*see also* Eriksson 1979a, Pöysä *et al.* 1994).

The overall mortality rate of common goldeneye broods in this study is comparable with previous studies (*see review in* Eadie *et al.* 1995). Brood mortality was age-dependent, being highest in the age-class I (1–23-day-old ducklings) (*see also* Pöysä & Virtanen 1994, Milonoff *et al.* 1995), which is a common phenomenon in several duck species (e.g. Ringelman & Longore 1982, Orhtmeyer & Ball 1990, Savard *et al.* 1991, Guyn & Clark 1999). Brood-specific mortality and lake-specific mortality varied in a similar way between the two brood age groups although these variables were based on partially different sample units (*see* Material and methods).

The lakes in our study area are relatively small, oligotrophic, and the proportion of lakes occupied by pike is high (Rask & Metsälä 1991, Raitaniemi 1995). Although the method used to estimate lake-specific pike predation risk was coarse we consider it reliable, because the index of pike predation risk varied considerably between the lakes and the rank of the lakes was consistent between the two study years. Also, the repeatability of the index of pike predation risk proved to be high. Similarly, Raitaniemi (1995) found that there was considerable variation in the number of pike caught between the lakes in the present study area.

In this study, the correlation between mortality of the young ducklings and lake-specific predation risk by pike was strong, implying that pike predation is an important source of mortality in young common goldeneye ducklings. Similarity of feeding sites between common goldeneye ducklings and pike may provide the explanation. Young ducklings feed in shallow water and capture freely swimming prey or prey well exposed on the bottom or on vegetation in open water near emergent plants (Eriksson 1976, Eadie *et al.* 1995). Similarly, adult pike are found in shallow and vegetated water in summer. Casselman and

Lewis (1996) suggested that very dense vegetative cover is suboptimal for pike, but the boundary zone between stands of aquatic vegetation and open water may provide important ambush hunting sites (*see also* Inskip 1982). On the other hand, there was no correlation between mortality of old ducklings and lake-specific predation risk by pike. This is to be expected, because larger and more mobile old ducklings may be difficult or even impossible for pike to catch. Furthermore, feeding habits of common goldeneye ducklings change with age from the preference of emergent plants near the shoreline to the preference of deeper and more open water where pike may not be so abundant (Eriksson 1976, Eadie *et al.* 1995, Nummi & Pöysä 1995b).

Beattie and Nudds (1989) suggested that avoidance of predatory fish is not an important determinant of habitat use by common goldeneye ducklings (note that they used ducklings, not females, in their experiment). Our sampling protocol of pike predation risk did not include the reference lakes and, therefore, we cannot say if tendency to avoid pike predation also influenced lake selection of common goldeneye broods. However, data of lake preference by the broods among the rearing lakes suggest that pike predation risk may not be an important factor in lake selection. For each of the rearing lakes that were studied in all of the thirteen years we calculated a simple index of brood preference as the total number of broods observed during the study. There was a positive, though not significant correlation between this index and the index of pike predation risk ( $r_s = 0.420$ ,  $n = 16$ ,  $p = 0.105$ ), indicating that, at least, common goldeneye broods did not discriminate against lakes in which pike predation risk was high. Furthermore, among the same lakes, the correlation between the index of lake preference and lake-specific mortality rate of ducklings in age-class I was positive ( $r_s = 0.572$ ,  $n = 16$ ,  $p = 0.021$ ). These findings suggest that, indeed, common goldeneye females probably were imperfect in predicting pike predation risk when selecting among the brood-rearing lakes. Pike predation may be considered as an unpredictable event during foraging activities of ducklings, implying that behavioural responses to avoid it may not have evolved.

In conclusion, our results provide evidence that foraging patch-related predation risk may decrease the quality of patches preferred in food acquisition by common goldeneye broods. Lakes selected for brood rearing by common goldeneye females were rich in food but also appeared to bring about varying predation risk that was correlated with brood mortality. Although females with broods invest in anti-predator vigilance (Ruusila & Pöysä 1998), the survival of offspring may largely be out of a female's control (see also Pöysä 1992, Pöysä *et al.* 1997). As the present results suggest, predation by pike appears to be such an unpredictable mortality factor. Of course, a female's ability to use its breeding environment successfully may vary depending on the age, prior experience, social status and physiological condition of the female. Also, the assessment of patch quality within a female's home range may improve with the extent of information gathered via habitat sampling before and during the current breeding season. Yet, because brood-rearing common goldeneye females are territorial and aggressively defend the brood territory from other females (Savard 1984, Eadie *et al.* 1995, Ruusila & Pöysä 1998), the best brood-rearing sites may be limited, hence, subordinate females may be forced to use brood-rearing sites where predation risk is high.

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