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Duck habitat use and reproduction in boreal wetlands: importance of habitat quality and population density

Sari Holopainen

Department of Forest Sciences
Faculty of Agriculture and Forestry
University of Helsinki

Academic dissertation

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Author: Sari Holopainen

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Thesis supervisors:
Dr Petri Nummi
Department of Forest Sciences, University of Helsinki, Helsinki, Finland

Professor Hannu Pöysä
Natural Resources Institute Finland, Joensuu, Finland

Pre-examiners:
Dr Matthieu Guillemain
Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice,
La Tour du Valat, France

Dr Toni Laaksonen
Department of Biology, University of Turku, Turku, Finland

Opponent:
Professor Anthony Fox
Department of Bioscience, Aarhus University, Aarhus, Denmark

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The boreal biome harbours a large share of the world's wetlands, and is the main breeding area for several duck species. Breeding habitats strongly influence duck reproduction. In this study, the habitat use of ducks and their breeding success was estimated in a boreal landscape in southern Finland. A review of duck habitat use in boreal wetlands was additionally made.

Boreal forest lakes are normally considered stable environments, but from a duck's point of view both resource abundance and habitat quality in the lakes may differ from one year to another. In this study the vegetation of boreal freshwater lakes was found to slowly change during the 20-year study period. Beavers (*Castor canadensis*) caused pronounced alterations in the lakes by flooding them. Flooding rendered lake vegetation structure more luxuriant and increased the lake use by ducks. In general, lake use by duck broods was positively associated with both the coverage of wide belts of tall emergent plants and the abundance of emerging insects and aquatic invertebrates. The relative importance of these factors varied between species.

The brood production of common goldeneyes (*Bucephala clangula*) was regulated by density dependence per se, but fluctuated with food availability per capita. No spatial density-dependent effects were found for the common teal (*Anas crecca*), but the breeding success was instead explained well by habitat quality variation. Both food and flood abundance had a positive effect, but different variables seemed to operate during different phases of the breeding season.

Many aspects of boreal breeding ducks are still poorly studied. Especially lacking are studies concerning duckling survival and the effects of anthropogenic actions on duck habitat use. This research underlines the importance of high quality habitats for breeding duck populations in the boreal landscape. The varying habitat requirements of duck species should be considered when implementing wetland management.

Keywords: common goldeneye, common teal, mallard, beaver, breeding success, population dynamics

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LIST OF ORIGINAL ARTICLES

This dissertation is based on the following articles, which are referred to by their Roman numerals. The articles I – IV are reprinted with kind permission of the publishers, while article V is author's version of the submitted manuscript.

I Suhonen S., Nummi P., Pöysä H. (2011). Long term stability of habitats and use by ducks in boreal lakes. Boreal Environmental Research 16 (suppl. B):71–80. http://www.borenv.net/BER/pdfs/ber16/ber16B-71.pdf

II Nummi P., Paasivaara A., Suhonen S., Pöysä, H. (2013). Wetland use by brood-rearing female ducks in a boreal forest landscape: the importance of food and habitat. Ibis 155: 68–79.
http://dx.doi.org/10.1111/ibi.12013

III Nummi P., Holopainen S., Rintala J., Pöysä, H. (2015). Mechanisms of density dependence in ducks: importance of space and per capita food. Oecologia 177: 679–688.
http://dx.doi.org/10.1007/s00442-014-3133-1

IV Holopainen S., Nummi P., Pöysä, H. (2014). Breeding in the stable boreal landscape: lake habitat variability drives brood production in the teal (*Anas crecca*). Freshwater Biology 59: 2621–2631.
http://dx.doi.org/10.1111/fwb.12458

V Holopainen S., Arzel C., Dessborn L., Elmberg J., Gunnarsson G., Nummi P., Pöysä H., Sjöberg K. A review of habitat use in ducks breeding in boreal freshwater wetlands. Manuscript.

Author's contributions

Sari Holopainen (formerly Suhonen) is fully responsible for the summary of this doctoral thesis. In study I she attended to data collection and made data analysis in addition to manuscript preparation. In study II she participated to manuscript preparation and had a minor part in data preparation. In study IV S. Holopainen was the main author and responsible in every stage from original idea to manuscript preparation. In studies III and V S. Holopainen attended to study design, was responsible in methods and implementation in addition to manuscript preparation. In review V S. Holopainen assembled the literature and was responsible for manuscript preparation.

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INTRODUCTION

Quality of habitats and individuals, as well as the degree of intra- and interspecific competition may vary and be reflected to the breeding success of the individuals of a species (Carrete et al. 2006; Begon et al. 2006). Population dynamics of animals depends on the effect of extrinsic and intrinsic factors working in the current moment or with a time lag (Newton 2003; Lande et al. 2002; Almaraz and Amat 2004; Begon et al. 2006). Basically, populations are thought to be limited by extrinsic factors, whereas intrinsic factors regulate populations.

Extrinsic, i.e. limiting factors are usually considered to be density independent, but they might also become regulating as a response to the population density (e.g. prey switching relationship, Brook et al. 2005). Extrinsic factors, in addition to intrinsic factors, can therefore cause variation in per capita birth or death rates along a gradient of population density. Extrinsic factors can affect population reproduction success during the breeding time or survival at any time of the year. The effectiveness of these factors depends on their extent and duration. Intrinsic factors regulate population dynamics via birth rate, death rate, immigration and emigration. The demographic characteristics of a population are also considered intrinsic factors (Newton 2003; Colwell 2010). The effect of intrinsic factors on population dynamics is likely to vary with fluctuations in population density and environmental conditions (Colwell 2010). For instance, the effect of competition on population fecundity varies in such a way (Wiens 1976). The relationship between vital rates and environmental effects (e.g. resources, stochasticity) or density-dependent regulation is the base for shaping the most optimal life history strategies (Cody 1971).

The way in which breeding success is manifested at varying densities depends on whether the species response takes place according to a process described by the Individual Adjustment Hypothesis (IAH) or the Habitat Heterogeneity Hypothesis (HHH). IAH competition is primarily exploitation competition for food, whereas competition in the HHH takes the form of interference competition for high quality space (Dhondt 2012). Earlier studies have shown that the populations of birds of prey, in particular, tend to behave according to HHH (Ferrer and Donazar 1996; Sergio et al. 2007; Krüger et al. 2012), but the same is also true for other species such as the great tit (*Parus major*, Dhondt et al. 1992) and mute swan (*Cygnus olor* (Gmel.), Nummi and Saari 2003). In HHH, some individuals have extremely low breeding success during high densities, while individuals occupying high quality territories do breed well. In IAH, individuals share the decrease in their breeding success during high densities; this effect is assumed to be mediated through intensified exploitation competition (Dhondt 2012).

Duck habitat selection during the breeding season

Levins (1968) argued that coevolution should exist between fitness and habitats, and also with the capacity of habitats to evoke settling behaviour. This is due to ultimate factors that work through survival and breeding success, and proximate factors working as “psychological factors” (Hildén 1965; Piper 2011). These habitat preferences can be innate or be based on imprinting to the particular habitat type where the individual is raised; possibly it is the combination of these two (Hildén 1965; Orians 1971).

According to general hypotheses natural environments are complex mosaics of patches, which differ in their quality in time and place (Hildén 1965, Levins 1968, Orians 1971).

From a species' point of view, good quality patches might be stable or varying depending on the species life history adaptations (Cody 1971; Benton and Grant 1996: Reznick et al. 2002). An individual maximises its fitness if it can successfully establish itself in an optimal habitat (Orians 1971; Piper 2011). However, the individual is limited by the time available for searching, by the probability to find a better patch and by the mortality rate during searching (Levins 1968). The possibilities of finding the best sites are high for ducks, but the question is how good the birds are in assessing habitats quality. The time available for habitat searching might also be restricted, especially at high altitudes and during brooding. The presence of other individuals of the same/different species can make the patch less suitable or even unavailable, or in some cases reveal the good quality of the patch leading to conspecific or heterospecific attraction (Hildén 1965; Orians 1971; Wiens 1989; Elmberg et al. 1997).

Migratory ducks are mobile organisms which have to resettle on their breeding environment every year. Moreover, the differing needs during the pair, nesting and brood stage and also within the brood stages shape the habitat use of ducks during the breeding season, thus causing temporal and spatial variation in habitat occupancy (Nummi and Pöysä 1993; Nummi and Pöysä 1995a). Brood rearing females, for example, move through the habitat mosaic when surveying good habitat patches matching the age-specific demands of the ducklings (Paasivaara and Pöysä 2008).

Boreal wetlands as duck breeding habitats

A large share of the worlds' ducks breed in the millions of lakes in the boreal biome, which harbours approximately 80% of the world's freshwaters (Schindler 1998; Mack and Morrison 2006). In North America, the wetlands of western boreal forests are the second most important duck breeding area after the prairies (Slattery et al. 2011). This importance of boreal areas might be even more pronounced in Eurasia (Hagemeijer and Blair 1997). Until recent times boreal areas have been less altered than more southern areas, but now human activities are increasing (Lee 2004; Mack and Morrison 2006; Slattery et al. 2011). Also climate change is affecting boreal wetland dynamics (Mialon et al. 2005; Riordan et al. 2006) and the ecosystems therein (Corcoran et al. 2009).

Boreal forest lakes are considered stable environments at the landscape scale, and their water level varies relatively little (Nummi and Pöysä 1993). Duck densities in the boreal wetlands are commonly low, but due to the large area of the boreal and rather stable water conditions its impact for duck populations is significant (Baldassarre and Bolen 2006). Many boreal lakes are too unproductive for duck habitat use and also have an unsuitable habitat structure, i.e. the ultimate features affecting the habitat selection in birds are not at an appropriate state (Hildén 1965). Invertebrate production is typically low in boreal lakes, and feeding in sharp-edged deep shores is not profitable for foraging of dabbling ducks and ducklings (Sjöberg et al. 2000; Nummi and Hahtola 2008; Nummi et al. 2012).

Even though boreal wetlands are rather stable at the landscape level, from a duck's point of view, ultimate factors such as resource abundance and habitat quality may differ from one year to another at the wetland level (Dessborn et al. 2009; Nummi and Holopainen 2014). For instance, wetland productivity may vary between years. This is because spring floods resulting from melting snow create seasonal shallow wetlands on lake shores and alter littoral net ecosystem productivity (Larmola et al. 2004). The formation of seasonal forest ponds (vernal pools) after snow melt might also offer important food-rich habitats for the ducks (Kattainen 2008). However, seasonal pond ecosystems and their dynamics in the boreal biome are poorly studied and waterfowl therein are especially devoid of studies (Paton 2005). The effects of pond duration in North American prairies has been studied extensively: temporary ponds that hold water just after snow melt benefit prairie breeding ducks at the beginning of the breeding season (Naugle et al. 2001). Seasonal ponds holding water during the summer are found to be especially important to dabbling duck breeding (Kantrud and Stewart 1977; Amundson and Arnold 2011). Shallow wetlands offer good foraging/nursery habitats for teal species during the spring (cinnamon teal, *Anas cyanoptera* (Vieill.), green-winged teal *A. carolinensis* (Gmel.): Isola et al. 2000; Taft et al. 2002) and summer (blue-winged teal *A. discors* (L.)*:* Swanson and Meyer 1977).

In the boreal biome, habitat amelioration by beavers (*Castor* sp.) benefits ducks by modifying oligotrophic, sharp-edged ponds into productive shallow wetlands. Facilitation is an aspect that has not been in focuse in community organization studies; conflicts and negative interactions such as competition and predation have been highlighted instead (Cherret 1989; Bertness and Callaway 1994). Currently more and more evidence has accumulated on the importance of positive interactions in natural communities (Hacker and Gaines 1997; Stachowicz 2001). These positive interactions include facilitation and mutualism (Stachowicz 2001), and they may be mediated through, e.g. ecosystem engineering (Jones et al. 1994; Nummi and Holopainen 2014). Facilitation may be especially important in oligotrophic boreal lakes. This is because the general model predicts that in low productivity patches facilitation by ecosystem engineering should increase productivity leading to increased species richness (Wright et al. 2002; Nummi and Holopainen 2014).

Duck species differ in their flexibility to respond to variation in environmental factors, such as habitat quality, habitat variability and weather (Koskimies and Lahti 1964; Wiens 1976, Nummi and Pöysä 1997). Common teal (*A. crecca* L., hereafter teal) is suggested to be a pioneer species that tracks and readily colonizes newly formed wetlands, while this response is slower in e.g. the mallard (*A. platyrhynchos* L., Nummi and Pöysä 1997; Nummi and Hahtola 2008).

In addition to yearly variation, the habitat structure of boreal wetlands experience a significant change within a breeding season and, thus, when the pairs arrive there is no emergent or aquatic vegetation that could work as stimulus of habitat structure (Svärdson 1949). However, the pair formation rate already may reflect the suitability of a habitat for breeding (Pöysä et al. 2001). The ability to forecast brood-stage food limitation by pairs has been found at least in mallard (Pöysä et al. 2000) and teal pairs (Elmberg et al. 2005). Finding invertebrate-rich habitats during the pair stage is crucial for incoming breeders like the teal as they cannot collect large lipid storages from their wintering and migration sites as capital breeders can (Krapu et al. 2004).The habitat quality of their breeding lakes can then cause variation in clutch size (Pietz et al. 2000; Krapu et al. 2004; Toft et al. 1982; but see Toft et al. 1984; green-winged teal). Because ducks usually extend their reproduction over several years, they can invoke the knowledge they have gathered from previous breeding seasons (Hildén 1965; Piper 2011). Successful breeding in the previous year might encourage females to lay their eggs in the same location again (Eriksson 1979; Clark and Shutler 1999). The local reproduction rate is thus determined by habitat factors affecting the breeding decisions of pairs and the survival of ducklings.

Breeding is an important phase during the course of the year as nesting success and duckling mortality are among the most influential factors affecting population growth rates (Hoekman et al. 2002; Coluccy et al. 2008). As already denoted, the ultimate factors affecting habitat-breeding- relationships in boreal lakes are especially pronounced, and many lakes are not suitable for pairs and are even less so for duck broods. In a study by Sjöberg et al. (2000) ca. 70% of lakes were used by mallard pairs, but broods used only ca.

30% of them. The lake use of teal pairs was found to be more evenly distributed, but broods used only 60% of the lakes; and, successful brood production was even more concentrated on a few lakes (Nummi et al. 2005). Difference in lake use is due to the food limitation in these lakes, and lake use with insufficient food resources would increase duckling mortality as showed experimentally by Gunnarsson et al. (2004, 2006). It seems that teals avoid brood-stage food limitation by congregating in beaver ponds where invertebrate production is high and the habitat structure favourable (Nummi and Hahtola 2008).

The aims of this thesis were to concentrate on the associations between the ducks and their habitat. My focus was in the boreal wetland ecosystems, their habitat structure and long term change. I studied the variation of different environmental factors such as food and flooding as well as duck densities. Finally I investigated the possible effects of these factors to duck population processes, including habitat use and population dynamics. I additionally assembled the studies concerning duck habitat use, breeding success and species richness in boreal wetlands to find the most important habitat variables and possible gaps in our knowledge.

MATERIAL AND METHODS

The Evo watershed area in Häme, southern Finland (61°12’N, 25°07’E) has been a target of long-term duck population studies and the environmental factors affecting them. There are 51 study lakes within a 39-km^2 area. Lake sizes vary between 0.1–49.5 ha and their combined shoreline is 49.9 km. The subsets of these lakes were used in different studies (**I**, 51; **II**, 12; **III**, **IV**, 50 lakes; one of the original 51 lakes was dropped because of increased cottage settlements). Lakes (usually) hold water throughout the brood period and freeze during the winter; some ponds have turned out to be seasonal in dry years and lose their waters during the latter part of the breeding season. The landscape in Evo represents a typical boreal forest zone in Finland and possibly throughout the Northern Hemisphere. The landscape consists mostly of state-owned forests that are in commercial use; lakes and bogs cover 10% of the area. Agricultural land is situated in one corner reaching the lakes of the study area. Human settlements are scarce. The largest settlement is located at the southern part of the area, where HAMK (the University of Applied Sciences) Evo campus (with. ca. 300 students) is situated. Stable waters experience occasional alteration by beaver flooding. Beavers typically dam the outlet of a natural pond, thus creating a flooded wetland. On average beavers remain at the same place for 3.6 years (Hyvönen and Nummi 2008). Beavers have yearly dammed 3–9 lakes (Nummi and Holopainen 2014).

Evo waterbird surveys have been organized by one person (PN) from 1989 to 2014. I have contributed to the surveys since 2009. Different time series sets of these data were used in different studies (**I**, 1989–1991, 2007–2009; **II**, 1989–1996; **III**, **IV**, 1989–2008). All the waterbirds in the area were surveyed, i.e. ducks, waders, gulls and divers. Pair surveys have been made every year after the ice melt, typically in the beginning of May. During the first study years there were two pair counts to catch the early and late migrators, but it was then realized that one yearly survey is enough for the area. Brood surveys were conducted five times in 1988–2008 (from June to August) and two times in 2009 (June and July). Each survey included a point count and a subsequent round survey in which the 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 Pöysä 1991). Species and sexes are recognized in the surveys, and the number and age of ducklings are defined (Pirkola and Högmander 1974). The duck species studied here commonly breed in the Evo area and are distributed widely in the boreal zone; mallard, teal and Eurasian wigeon (*Anas penelope* L.) are dabbling ducks and the common goldeneye (*Bucephala clangula* L., hereafter goldeneye) is a diving duck.

In addition to duck surveys, Evo has been the subject for several long-term environmental studies. The focus has been on food availability and habitat structure. The vegetation of the lakes has been measured in 1989 and re-measured in 2009. Vegetation type, width and height were observed during the July brood surveys. Observations were written down in the maps and the portions of different types calculated afterwards. Lake shore depth was additionally measured. These parameters were used together with lakes size to compose a habitat luxuriance gradient with principal component analysis. This gradient is biologically meaningful, with small sparsely vegetated and deep shored lakes at the one end of the gradient and large lakes with abundant vegetation and shallow shores at the other end. This gradient thus reflects the common idea of the suitability for ducks (Kauppinen 1993). Long-term data sets enable studying the stability in habitat structure in terms of vegetation, lake size and shore depth in 51 lakes (**I**, also used in **II**).

Invertebrate trapping was conducted in the lakes in June–July 1989–2008 (**III**, **IV**, but 1989–1996 in **II**). Invertebrates reflect the food production of the lakes. Originally 12 of the 51 Evo study lakes were selected for invertebrate sampling so that they would cover the whole habitat luxuriance gradient (Nummi and Pöysä 1993). Lakes were chosen based on the habitat measurements performed in 1989. Lakes that had not faced a sudden change in their gradient status (e.g. beaver occupancy, change in fish status due to recovery from acidification: a total of 7 lakes) were used for the invertebrate index as a measurement for the yearly varying food abundance of the area (**III**, **IV**, Nummi and Hahtola 2008; Nummi et al. 2012). This is because we wanted the lakes to give a general representation of the food situation in the area. The seven lakes included in the food resource monitoring represented well the average luxuriance of the study area lakes, although the most barren lakes were missing. However, we were still able to recognize the variation through time. Dessborn et al. (2009) found that the number of emerging chironomids per lake varied considerably between years, but despite this variation the order of the lakes in respect to the chironomid abundance was rather stable.

All details of the trapping procedure were identical between the lakes. Free-swimming aquatic invertebrates were trapped with the activity trap described in Murkin et al. (1983). Because fish affect the activity trap catch, traps with fish were omitted from the analyses (Elmberg et al. 1992). Emerging insects were captured with emergence traps similar to those described by Danell and Sjöberg (1977).

Four traps of each type were used per lake. The traps were placed at two fixed sites on the shore so that seemingly the best shore section with wide and high vegetation and the poorest shore section with a narrow or non-existent vegetation belt was sampled in each lake. The food abundance in a given lake was thus measured in two ways: in terms of the index of free-swimming invertebrates and in terms of the total number of emerging insects. These two food abundance measures were combined to get an overall study area-level food abundance index (**III**, **IV**). The index value varied considerably at the beginning of the study period, but was rather stable during the latter part of the period. Over the long-term, the index showed a slight decrease. For the study where we wished to show differences in the food items of different species (**II**), we divided the emerging insects into two groups, large (Ephemeroptera, Odonata, Trichoptera) and small (Diptera).

For the habitat use review (**V**) the data set was collected by searching peer-reviewed articles from the Web of Knowledge and from the reference lists from the retrieved articles. Searching concentrated on duck species living in boreal freshwater wetlands (Mack and

Morrison 2006; Wells and Blancher 2011; BirdLife International 2014). I only used the articles that analysed habitat use, habitat-based survival and species richness of boreal breeding ducks at the lake-level (i.e. 3rd order habitat selection *sensu* Kaminski and Elmberg 2014). I additionally searched papers describing breeding success and nest site selection at the macro and micro (4th order habitat selection) habitat scales. The boreal biome was defined according to Mack and Morrison (2006) in North America, and Taggart and Cross (2009) in Eurasia. With this framing the boreal consists of Alaska and larges shares of Canada, Fennoscandia, northern parts of Baltic and large portions of Siberia touching China near the Pacific Ocean.

RESULTS AND DISCUSSION

It has been stated that identifying the limiting life history stage is often crucial when the goal of an ecological study is to determine the factors restricting the distribution of a species (Bruno 2000). Breeding success has been found to be important in modifying the population dynamics of some dabbling ducks, e.g. the mallard (Hoekman et al. 2002; Coluccy et al. 2008) and wigeon (Gardarsson et al. 2008). It is likely that it is the duckling stage that limits the occurrence of ducks in boreal wetlands, as suggested by the higher survival of teal broods in beaver flowages (Nummi and Hahtola 2008), the increased survival of mallard ducklings with additional food (Gunnarsson et al. 2004) and limited fledgling production by goldeneyes despite the increase of nest boxes and number of pairs (Pöysä and Pöysä 2002).

Long-term habitat change and habitat structure

The habitat structure of boreal lake systems was shown to be rather stable in the long term and at the landscape scale (**I**). Lake habitat structure in the lakes had not changed systematically between the study periods. However, there were some notable lake-specific changes: lakes that had become more luxuriant, i.e. their emergent vegetation increased, were influenced by humans. Lakes that had become poorer, i.e. their emergent vegetation had decreased while forest and *Sphagnum* shores had increased, were small forest lakes. In addition, beaver flooding caused pronounced alterations in the lakes making them more luxuriant during the flooding. This facilitation by the beaver created good quality habitats for ducks (**I**, Nummi and Holopainen 2014). Facilitation is suggested to take place when one species has a beneficial effect upon another species (van der Wal et al. 2000; Machicote et al. 2004). One such process is facilitation through habitat modification (Power et al. 1996), which is the case with the beavers.

In the context of the availability of lakes with different habitat structure luxuriance, I studied the habitat use of three ducks commonly breeding in the study area (**I**). The habitat use of ducks reflected the changes in the lakes and in the population sizes. Increasing goldeneye pair numbers and decreasing teal pair numbers explained the number of lakes used by them, but did not explain the luxuriance variation of the used lakes. Especially beaver activity increased the lake use of the ducks. Even goldeneye broods congregated in beaver ponds, even though the species is territorial during the brood stage. If the loss of emergent vegetation and the increase of *Sphagnum* shores continue in forest lakes, the number of structurally suitable lakes for the ducks will decrease in the area. Facilitation by the beaver might thus be an increasingly important mechanism that from the ducks point of view increases the quantity of suitable lakes in the area.

Habitat associations of sympatric breeding ducks

According to the competition theory, sympatric ducks cannot consume identical resources, but they are confined to species-specific optimal environments (Hildén 1965; Toft et al. 1982; Cody 1985). My study found important differences between the habitat associations of sympatric duck species during the brood-rearing stage (**II**). Although lake use by duck broods was related to habitat structure (wide belts of tall emergent plants) and food abundance (two size classes of emerging insects and aquatic invertebrates), their relative importance varied among species (Fig 1).

Aquatic invertebrates were the most important factor associated with wetland use for goldeneye broods, which was an expected result for the diving duck. Surprisingly, also large emerging insects showed high importance. The result that goldeneye did not associate with habitat structure is supported by an earlier study, which showed that goldeneye uses barren lakes through the breeding season (Nummi and Pöysä 1993). Interesting differences between teal and mallard were found in food-related habitat use. Observations of the teal broods were more abundant on lakes with greater dipteran emergence whereas habitat structure and large emerging insects were important for the mallard. This might also explain the temporal difference of these species in inhabiting newly created patches (Nummi and Pöysä 1997; Nummi and Hahtola 2008). Small invertebrates increase first, after which thricopterans and other large insects increase (Danell and Sjöberg 1982; Nummi 1989).

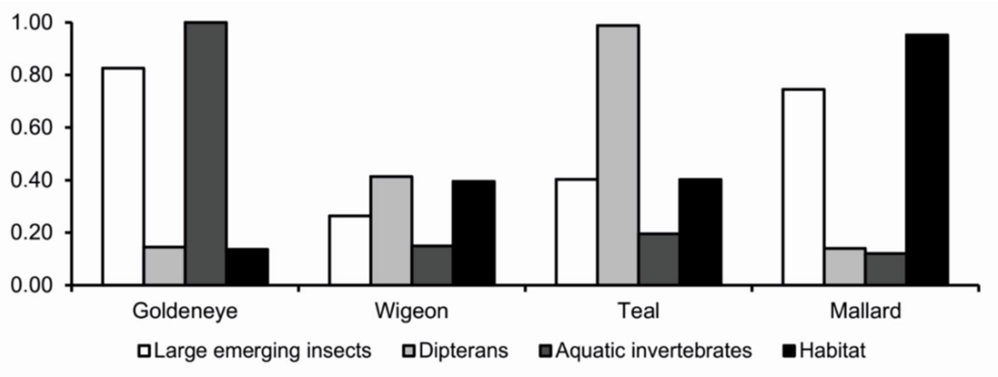

Figure 1. Relative importance of habitat and food variables in explaining the habitat use of brood-rearing female ducks. Importance value is the sum of the Akaike weights for each variable across all models where it occurred (for more details, see **II**).

The occurrence of wigeon broods was related to emerging Diptera and habitat structure, but the associations were not strong. The uncertainty partly results from the low numbers of wigeon broods. In the Evo study area wigeon broods have disappeared nearly completely during recent years, possibly reflecting changes in the habitat quality. Unfortunately, the ultimate factors affecting the habitat associations of breeding wigeon remain poorly known. More knowledge of wigeon breeding is thus much needed as the brood production of the species has been declining in Finland as a whole (Rintala et al. 2014).

The effects of density and a varying environment on breeding success

Occurrence of density dependence in animal populations has commonly been looked for using time series analyses, but the mechanisms of density dependence usually remain unknown (Viljugrein et al. 2005). However, knowledge of these mechanisms would help to understand how the populations are limited and regulated. This knowledge could also be used in developing applications in management and conservation.

My study (**III**) showed that the habitat use of goldeneye is much more predictable from year to year than that of the teal. This is in agreement with the idea that the “slow”-species of the continuum often live in more stable habitats. Populations may thus approach the carrying capacity of the environment which may result in clear density dependent feedback, especially in territorial species (Sæther and Engen 2002; Elmberg et al. 2003; Pöysä and Pesonen 2003). The teal is an example of the “fast” species that typically lives in habitats that are either unpredictable in time or are short-lived, and are themselves short-lived (Nummi and Pöysä 1997; Sæther and Engen 2002). Species with highly varying populations are limited by environmental resources and should be capable of reaching high reproduction rates during favourable times (Fowler 1981; Sæther et al. 1996).

The results revealed that different regulation mechanisms were operating in the studied species (**III**). Competition over space and food limit goldeneye brood production, while the teal was not affected by density *per ce*, but by *per capita* food limitation. In high densities some species occur in a broader range of habitats and thus some individuals are forced to breed in less-suitable habitats (Svärdson 1949). The number of used lakes in Evo indeed reflected the population size of the duck species (**I**). According to my results, goldeneyes followed HHH; at high densities some females had extremely low breeding success, and they possibly did not breed at all. In the Evo area this means that while the goldeneye population has increased, the number of broods produced in the area has not. This theory is also supported by the observation that an increase in nest boxes will increase the number of breeding pairs, but not the number of fledglings (Pöysä and Pöysä 2002). Instead, I found that the number of broods produced in Evo was varying with the *per capita* food abundance, and in years of abundant food the proportion of brooded pairs increased. In teal the effects of exploitation competition may gradually build up during the course of the brooding period. The increase of food supply *per capita* increased the proportion of brooding pairs. However, the increase was gentler than in the territorial goldeneye, reflecting the operation of some other factors.

The variation in food abundance and predation is suggested to explain the breeding success of teals in the boreal wetlands (Elmberg et al. 2005).Variation in the reproduction output of the teal was relatively high in our study area, and I used pair density, habitat and weather variables to explain it (**IV**). I used two brood age classes to reveal factors operating at different stages of the breeding season. The number of broods in both age classes was explained well by habitat quality, but different variables seem to operate during different phases of the breeding season. An increase in abundance of breeding pairs and of food led to increased production of younger broods supporting the results of my other study (**III**). Habitat factors including the amount of food and floods (i.e. beaver and spring) were the most important predictors for the production of older broods, which are more influential in terms of recruitment. Results show the importance of good quality disturbed habitats for teal, even though their aerial cover is only marginal. Up to 65% of the Evo teal broods congregate in beaver-flooded areas, which comprise only 7% of the waters (Nummi and Pöysä 1995b). The increase of invertebrate food and favourable habitat structure i.e. the increase of shallow water and vegetation cover are apparently the reasons supporting teal brood production (see also **I**,**V**) (Beard 1953; Longcore et al. 2006; Nummi and Hahtola 2008).

In addition to beaver floods, also spring floods create seasonal disturbance habitats, and as was shown, they increased the number of teal broods. The effect of seasonal ponds on duck breeding success has previously not been found from the boreal biome, while this interplay is well known in e.g. the prairies (Krapu et al. 2000; Pietz et al. 2000). The area of seasonal wetlands is large in the boreal biome (Mialon et al. 2005; Kattainen 2008), and because they have found to be exceptionally invertebrate-rich patches (Kattainen 2008), they might thus need more attention in the population dynamic studies concerning ducks. While the occurrence and quality of seasonal ponds is an aspect that has been poorly studied in the boreal biome, it is a timely subject. It is expected that due to climate change the snow pack of boreal areas will become thinner (Räisänen and Eklund 2012) and changes in snow cover will strongly influence wetland dynamics (Mialon et al. 2005). The way in which climate change affects annual wetland dynamics via snow cover thickness and extent might be area-dependent and, thus, lead to variation in the seasonal wetland area (Mialon et al. 2005). However, boreal pond shrinkage has already been observed (Riordan et al. 2006). In addition to the direct habitat loss, ducks breeding success might suffer a climate warming caused mismatch (Drever et al. 2012).

Duck habitat use and breeding success in the boreal biome

The review of habitat selection studies on ducks breeding in the boreal wetlands revealed several crucial gaps in our knowledge (**V**). Almost half of the boreal biome including Siberia lacked peer-reviewed scientific literature, while North America and Fennoscandia were well represented. Few species dominated among the studies and several species were not addressed in any studies. The most positive associations with duck habitat use were found from food resources, habitat structure, and facilitation by beaver, although duck guilds expressed some differences in how they were affected by different factors. However, these findings underline again the effect of ultimate habitat factors in boreal wetlands. From commonly studied variables, water characteristics did not usually have an effect on duck habitat use or survival. Serious gaps were found from the effects of anthropogenic acts on the habitat use and breeding success of boreal breeding ducks at the terrain level. Based on the suggestions in larger scale studies measuring the decrease of boreal breeding duck populations, one possible reason for the decline could be human-caused habitat changes in the boreal biome (Francis 1994; Afton and Anderson 2001). The nesting site characteristics of dabbling ducks are additionally poorly known, although some information about their nest and hatching success exists. As boreal environments are suggested to be more and more affected by anthropogenic use in addition to climate change (Schindler 1998; Riordan et al. 2006; Mann et al. 2012), the review underlines the need for studies on how these acts are reflected to the habitat use and breeding success of ducks.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

As a conclusion, this thesis produced new information about the habitat-breeding relationship of ducks and the long-term changes in boreal lake habitats. Lake habitat structure only experienced slow changes, which were accelerated mainly by habitat modification by the beaver (**I**). The enhancement of variables linked to ultimate habitat selection factors are crucial in barren boreal wetlands. The variation in yearly food abundance affects the number of broods produced (**III**, **IV**, **V**). Seasonal wetlands and beaver ponds appear to be food-rich patches for the ducks and regulate local brood production, especially concerning the teal (**IV**, **V**). My studies revealed clear differences between species in the food-related habitat use (**II**). Such detailed studies concerning factors underlining the habitat use of boreal breeding ducks are rare, in particular when it comes to the different stages of the breeding season (**V**).

The review (**V**) showed that more studies should be performed, particularly concerning the different threats to boreal breeding ducks due to anthropogenic effects in boreal wetlands, both direct (e.g. forestry, hydroelectric development and recreational activities) and indirect (e.g. climate change) (Austin et al. 2000; Mack and Morrison 2006; Savard et al. 2008; Mann et al. 2012; Guillemain et al. 2013; Morissette et al. 2013). For now our knowledge is limited, which might reflect the underestimation of the significance of boreal wetlands as breeding areas in the past, and the few human development activities when compared to more southern areas (Mack and Morrison 2006). The review also showed that the influence of wetland isolation on duck habitat use in boreal areas is poorly know, even though this information might be valuable for wetland conservation and restoration programmes (Beatty et al. 2014; Sebastian-Gonzalez and Green 2014).

In duck management it is essential to understand the habitat factors affecting duck distribution. Changes in these habitat factors and the possible consequences to population processes must additionally be recognized (Baldassarre and Bolen 2006). Habitat selection by ducks may be related to single or interacting features of habitat characteristics and will be interacting with breeding success. In successful management the mechanisms that address the breeding success should be considered. For example, the increase of nest boxes for goldeneye may not increase breeding success, if it is limited by direct density dependence or by food availability (**III**, Pöysä & Pöysä 2002). Instead, teals can congregate in high densities in small areas and produce broods successfully if food is abundant. Abundant vegetation structure is the ultimate factor framing the wetland use of the wigeon and mallard (**II**, Nummi & Holopainen 2014).

The varying habitat requirements of common duck species could influence the success of wetland management programs, and these factors may be particularly important for initiatives aimed at harvested species or species of conservation concern. My research underlines the importance of high quality habitats for breeding ducks in the boreal forest landscape. The existence of these habitats depends substantially on human actions, such as managing beaver populations and preserving seasonal pond habitats. Wetland destruction by humans began long ago and has accelerated in recent times (Gibbs 2000; Amezaga et al. 2002). Apart from direct wetland destruction, climate warming (McMenamin et al. 2008) and the over-exploitation of beavers (Naiman et al. 1988; Nolet and Rosell 1998) have indirectly affected the amount and distribution of wetlands. Holarctic landscapes have been in an unnatural state lacking beaver-created wetlands, but the beavers have recently begun to return and restore the wetlands of their former range (Nolet and Rosell 1998). In habitat conservation and restoration, it might wise to identify probable keystone species or ecosystem engineers and focus on their management (Ebenman and Jonsson 2005; Byers et al. 2006). In barren boreal lakes beaver flooding might increase the number of lakes available for ducks, e.g. for the habitat structure-dependent mallard and wigeon (**I**, **II**, Nummi and Holopainen 2014). Thus, by promoting beavers in restoration one could affect the enhancement of important ultimate factors assigning the habitat use and breeding of ducks.

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