Habitat Use of Waterfowl Assemblages

in Viikki Reserve:

A Comparison of Grazed and Ungrazed Shorelines

A Thesis submitted for the MScFB degree in Forest Ecology,
Specialization: Wildlife Management

University of Helsinki

Department of Forest Sciences

May 2013

Ladan Samooty
Domestic cattle grazing as a disturbance factor to the vegetation structure is investigated. It is concluded that the process of heterospecific attraction plays as important a role as vegetation structure in predicting waterfowl assemblage patterns. The study site, an estuarine wetland in an urban zone in Helsinki, is studied during one staging period. Two sets of shorelines are focused on, grazed and ungrazed. Avian assemblages are compared in both types of shorelines based on variables of community structure and habitat resource use. The two most influential variables are aquatic invertebrate biomass index as food supply, and bare shoreline proportion as habitat structure indicator. The process of competition as regulating factor in forming avian aggregations is ruled out by confirming that sufficient amounts of habitat resources, food and space are available. The co-occurrence patterns of foraging guilds are analyzed. Heterogeneous vegetation structure, combined with social attraction, influences avian distribution patterns. Niche partitioning is absent across the whole landscape as invertebrate food resource is not a limiting factor. Microhabitat use within plots is evenly distributed. The constantly popular microhabitats are sections of the grazed shorelines where resource partitioning is absent. Avian habitat preferences are shaped by extent of available bare shoreline and the presence of other waterfowl. The latter effect is confirmed both as conspecific and heterospecific attraction. It is the first time this wetland, which is also a designated Natura 2000 and Ramsar site, is being investigated for wildlife community dynamics. The site does not suffer from major environmental threats and has potential for more waterfowl consumers. In view of its international significance, this and similar research can aid urban planners in Reserve management to enhance avian diversity towards attracting species of more conservation concern.
To my parents
Acknowledgements

I sincerely thank the Environment Center of the City of Helsinki for giving me the opportunity to access the Reserve, and to conduct the field procedures.

My warmest gratitude to Professor Kari Heliövaara and an external anonymous reviewer for taking the time to evaluate the present work.

I am tremendously indebted to Dr. Petri Nummi for designing the study, materializing my research interest into a workable project, and offering constant support and guidance at every step of the task.

Dr Veli Matti Väänänen kindly provided me with many useful hints on field methodology, constructive encouragement on the subject matter, and facilitating access to equipment.

I always benefited from the insightful remarks of Eero Haapanen, my field collaborator, in the many discussions we had on waterfowl ecology and wetland management. It was owing to his organizational and terrain skills that the research was conducted successfully.

Dr Michael Starr and Dr Eshetu Yirdaw presented me with priceless feedback and substantial advice on the preliminary manuscript.

My cordial appreciation also goes to Dr Hannu Rita for the challenging workshops and the motivating discussions.

Special thanks to an amateur naturalist with no formal background but with extensive field experience who provided the following comment, thus summarizing several of the points I discuss here,

“Surely dependency on specific shorelines denotes the type of foods required by each species and by this, I mean Geese like grass and terns like lug worms, sand eels, etc. Waders like short vegetation and water plants ... It also depends on the seasonal breeding cycle of individual species. Some, like the tern, prefer bare stones to lay their eggs; while geese like dead grass to build a nest and fresh growth for the young as they feed [independently] from the first day. ... So put sheep where geese will follow and goats where seabirds follow.”
# Table of Contents

1. Introduction  
   1.1. Background ................................................................. 1  
   1.2. Theoretical Framework .................................................. 2  
   1.3. Research Topic and Objectives ....................................... 8  

2. Previous Research ............................................................ 9  
   2.1 Habitat Preferences of Waterfowl ..................................... 10  
   2.2. Aquatic Macroinvertebrates .......................................... 11  
   2.3. Aquatic Macrophytes .................................................... 12  

3. Material and Methods .......................................................... 13  
   3.1. Study Site .................................................................... 13  
   3.2. Study Plots .................................................................. 14  
   3.3. Invertebrate Sampling .................................................. 15  
   3.4. Waterfowl Monitoring ................................................... 16  
   3.5. Vegetation Observations ............................................... 17  
   3.6. Abiotic Parameters ....................................................... 18  
   3.7. Data Analysis .............................................................. 18  

4. Results ................................................................................. 20  
   4.1. Aquatic Macroinvertebrates ............................................ 20  
   4.2. Shoreline Vegetation Structure ........................................ 22  
   4.3. Avian Assemblages ....................................................... 23  
   4.4. Zonation of Activities ................................................... 29  

5. Discussion ............................................................................. 31  
   5.1. Trophic Cascades .......................................................... 32  
   5.2. Waterfowl Preferences .................................................... 34  
   5.3. Factors Affecting Aquatic Macroinvertebrates ..................... 35  

6. Conclusions ........................................................................... 36
List of Figures and Tables

Table 1. Details of bird groups used in this study ........................................ 5
Fig. 1. Study plot features ................................................................. 15
Fig. 2. Layout of Study Plots ............................................................ 16
Table 2. Comparison of 3 test results ................................................... 20
Fig. 3. Distribution of macroinvertebrates by taxon .............................. 21
Fig. 4. Relationship between consumer and food supply ..................... 23
Fig. 5. Total waterfowl abundance per plot. .................................... 26
Fig. 6. Effect of bare shoreline on assemblages ................................ 27
Fig. 7. Difference in abundance of birds in plots .............................. 28
Fig. 8. Temporal fluctuations in population .................................... 30
Fig. 9. Proportion of activity per plot ............................................. 31
The heron whimpered next,
“My misery prefers the empty shoreline of the sea.”

(Conference of the Birds, Attar, 1145 -1221 AD)
1. Introduction

1.1. Background

The present work is a research report on how the disturbance by grazing domestic cattle on vegetation structure affects waterfowl habitat use of a wetland, specifically foraging. Two sets of treatment and control plots were devised. Avian habitat use, assemblages, and related parameters were recorded. Through gradient analysis of several biotic and abiotic parameters, a number of observations were made and some patterns of assemblage in micro-habitat use emerged for the consideration of wetland management with biodiversity conservation in mind. Microhabitat partitioning was confirmed within plots, but not across plots in routine daily activities. Waterfowl abundance was sharply skewed to the side of the grazed plots.

Wetland management has extensive roots in human civilization. For instance, a brief look at ancient history reveals since the earliest human settlements on Earth, human beings on Mesopotamia and Nile river delta were witness to how populations of wintering waterfowl fluctuated with specific causes related to the natural system of the Fertile Crescent. The presence of a cause and effect phenomenon between waterfowl and their habitat is therefore not a novel discovery. The ancient Egyptians’ fascination with preserving aquatic avian specimens and keeping their census can be indicative of having detected ecological patterns, and most likely their ecosystem management attempts. In the very beginning of a major reference on wetlands, it is reminded that both early civilizations and “immense human suffering” is indebted to wetlands. (Keddy 2000, p.3)

In the current times, one of the earliest instances of modern research on the importance of vegetation structure for waterfowl and nesting distribution was presented in the book *Nesting birds and the vegetation substrate* (Beecher 1942). In an extensive literature review, Kantrud (1985) mentions 12 studies between 1935 and 1982 confirming waterfowl general avoidance of dense vegetation cover, and attraction to non-vegetated open mudflats. In the same literature review, reference is made to 8 studies between 1941 and 1982 which proved waterfowl attraction to wetlands with alternating patches of open and vegetated water.
Importance of Wetlands. It is an established fact that wetlands play a significant role in regulating the hydrological cycle, controlling floods, facilitating nutrient cycling, moderating temperature, providing habitat for wildlife, and all benefits derived from ecosystem services. Protecting and enhancing their ecosystem health is therefore as important as regulating global climate change. They can act as natural structures to prevent and control flood waters and are economically much more effective than man-made structures, hence their attraction to modern property market policies. (Boyd & Banzhaf 2007). From a wildlife management point of view, wetlands are important in providing waterfowl with year-round or seasonal refuge, breeding, nesting, and foraging grounds. Three functional groups of wildlife, i.e. fish and shellfish; waterfowl and other birds; furbearers are indispensably dependent on wetlands as their habitats. (Tiner 1984, p.13).

1.2. Theoretical Framework

The general realm of this research is within the boundaries of community ecology, with implications for wildlife management in coastal ecosystems. Community ecology is concerned with detecting patterns among assemblage members and relating them to underlying processes, natural mechanisms, and other causes. Likewise, this work analyzes the waterfowl assemblages by comparing their behavioral responses in habitat resource use, and attempts to find the underlying driving causes in inducing such responses.

The conceptual approach to community ecology in this work complies with how Whittaker defined a community, as “an assemblage of different taxa living in one environment, interacting in one system” (as cited in Wiens 1989, Vol 1, p.3). The MacArthurian view that geographical proximity is the major factor in linking assemblages has been considered, but much more emphasis has been placed on Whittaker’s theorem. It has been assumed that the waterfowl in this study have the advantage of relocating to adjacent micro-habitats, and that they are not restricted to one habitat patch at the local scale. Their assemblage is not due to necessity but of choice, and the interspecific interactions are not blind causes of geographical proximity, but of heterospecific attraction in the absence of habitat resources shortage. This point will be elaborated later on in this work.
Moreover, reference should be made to the two extremes of Clements community as one purposeful integrated organism composed of dependent species, and Gleason community as an accidental non-integrated gathering of independent species. Here, a mid-way approach has been adopted, i.e., presuming the studied waterfowl community is an inter-woven system of dependent individuals; at the same time recognizing the element of stochasticity in changes to the system (Wiens 1989, Vol 1, pp 5-7).

A note about terminology is necessary to mention here. *Aggregation* denotes the linear dispersion and spacing scheme of individuals on a system of linear coordinates. (Ricklefs & Miller 2000) Thus, this term in its strict ecological sense is not applicable to the present work as the scope of the study did not include specifying the geographic location of the occurrence of individuals in the study plots, nor did it include the spatial patterns of individual distribution in relation to the other individuals. Aggregations denote important facts about habitat suitability as an evolutionary response or as a purposeful immediacy, social disposition in resource use, and population defense mechanisms against predation and allospecific competition (*ibid*). Although the above are extremely revealing in a study of communities, this is one potential that was not covered in the present research.

*Community Dynamics, the Guild.* Observing, recording and predicting the spatial and temporal patterns of a community and modeling the heterogeneity of its populations and their demographic composition is a well-challenged interdisciplinary field, frequently used in landscape and community ecology. Coexisting populations in a community are in a dynamic process of interaction with each other. The processes of environmental changes, immigration, dispersion, predation, competition, colonization, and extinction shape the mechanisms involved in population dynamics of a community. Based on the terminology proposed by Fauth *et al* (1996) community interactions can be studied from different angles, based on which of the following components are considered as a set: geography, resources, and phylogeny. The focus of this paper is on assemblages, groups of individuals that are taxonomically related closely and occur in the same geographical area.

Taking another set of interactions, resources and geography, a guild is formed. In a guild, the emphasis is on how some resources are identically used by populations of
different taxa occurring in the same location. Wiens defined guild as a structural feature to describe community grouping of involved species by “ecological similarities in hierarchical clusters” (1989, Vol.1, p.156). These similarities are determined by how resources are used rather than by how species are related taxonomically. According to MacMahon and Jakšić (as cited in Wiens 1989, Vol.1, p.158), a guild should be defined as all of the species using a resource in a similar manner, and this implies effect of consumer use on the resource. Also, Root interpreted guild as a clustering of species overlapping in utilizing a resource. For example, Pöysä (1983) studied avian communities of a eutrophic lake in Finland, and based his study on two different guild categories, one based on feeding habitat characteristics and the other on feeding methods. The former produced three guilds, and the latter five guilds. The result of these two sets combined, resulted in a guild of only two clusters. Finally, guild classification is arbitrary and relative to the study objectives, but is always due to ecology and/or morphology of the organisms concerned. The important concluding remark is that guild determination is relatively arbitrary and subjective depending on which ecomorphological features and which species are taken into account as analysis parameters. Moreover, depending on environmental factors, response of identical individuals can vary from one habitat to the other.

Methodologically, there are two categories of approaching guilds, a priori and a posteriori. The former designates beforehand a set of criteria to fit the observed features of individuals, mostly on foraging behavior, location, diet characteristics, and ecomorphological features. A posteriori methods use multivariate statistical analyses (such as cluster analysis, PCA, canonical correlation, DFA, and Euclidean distance) to decide which species share the most similarities in terms of quantitative features. Wiens discusses the most reliable method is to combine qualitative and quantitative data to obtain the most objective results (Wiens 1989, Vol.1, p.176). He also claims that no a priori guild categorization has been confirmed by an a posteriori analysis to verify the guild clustering is correct (Wiens 1989, Vol.1, p.164). A probable shortcoming in the present work is the lack of this complementing to enhance results, and avoid systematic errors due to subjective bias.

Guilds on feeding behavior are especially revealing about how and why individuals in a community are related to each other. This is the basis of five groups of waterfowl
in this study. With respect to waterfowl, Wiens (1989, Vol.1, p.214) mentions the guild “teal-mallard-pintail-swan” formed on the basis of neck length grouping and further specified by feeding depth. He also makes reference to a study of swans in Scandinavia where swans are included in the Dabblers guild. (ibid) In the waterfowl assemblage here, I recognized four guilds based on foraging location, and then on habitat structural difference in using the same food resources, i.e. Dabblers-divers, Waders, Geese, Swans. One guild was formed due to the limited type of resource used, which is seabirds feeding exclusively on fish. Therefore five guilds (referred hereafter as group) are compared in the above assemblages.

From a taxonomic point of view, these five groups are compatible with the taxa as summarized in Table 1. Divers and dabblers were placed in one group as their foraging habits in preferring open waters is the same, although the physical posture in obtaining the food differs in them. Due to feeding on small fish, divers are also seen in deeper waters than dabblers. But these differences could be ignored for the purpose of this study and both were placed in the same guild. Contrary to this, although swans and geese are both taxonomically close members of the Anatidae family, they were placed in separate guilds based on their observed distinct foraging locations. Initially, both were placed in the same guild; however, it was noticed having them in two separate groups revealed distinguishing responses that would otherwise remain undetected.

Although in some studies Grey Heron (Ardea cinerea) is included in the Wader guild, I found it more appropriate to consider them in the Seabird group, as both taxa feed on larger-sized fish (For example in Weller 1995). The waders in this study were mostly shoreline birds, feeding on invertebrates.

Table 1. Details of bird groups used in this study

<table>
<thead>
<tr>
<th>Bird Group</th>
<th>Taxonomic Nomenclature</th>
<th>Taxonomic Hierarchy</th>
<th>Observed Species in the study site</th>
</tr>
</thead>
<tbody>
<tr>
<td>Divers</td>
<td>Aythyinae</td>
<td>Subfamily</td>
<td>Podiceps cristatus, Mergus spp</td>
</tr>
<tr>
<td>Dabblers</td>
<td>Anatinae</td>
<td>Subfamily</td>
<td>Anas spp, Bucephala clangula, Fulica atra, Aythya spp</td>
</tr>
</tbody>
</table>
In quantifying the characteristics of these assemblages, I adopted the common parameters of community structure, as summarized by Ricklefs & Miller (2000) species richness, relative abundance, vegetation structure, and trophic relationship. However, to combine the aspect of guild in the comparison, species is replaced by guild. The idea of trophic relationship is also approximately embedded in the guild grouping.

The recorded behavioral responses to habitat use were based on observed activities of waterfowl during daytime. Five categories of behavioral responses were recorded and analyzed. These were foraging, preening, resting, sleeping, and other. ‘Other’ includes activities that are of less importance to this study. They include: preying, exploring, guarding, playing, and crossing.

*Community Dynamics, Zonation.* Keddy (2000, p.106) claims that animal distribution is not decided by their physiological requirements, but by interspecific competition. It is the ecological processes that cause zonation. He specifically mentions wetland plants as a factor in forming zonation patterns in avian assemblages. He argues that zonation provides ready-made patterns for observation, especially on avian composition. In the present study, different shorelines are considered as micro-habitats, and the overall strip of adjacent land to water is considered the habitat landscape. Therefore, it is targeted to identify avian zonation patterns across shorelines to predict distribution and habitat use, and to finally make inferences about habitat preferences.

On the other hand, Wiens (1989, Vol.1, p.48) stresses the importance of edges of plot boundaries in affecting habitat use. He argues that if a certain bird species prefers edges, its presence will be favorably represented in small plots, while the more cryptic species will be under-represented in the same plot. This has been noted in the
field data collection for this work and every effort was made to detect all individuals present, specifically in the densely-vegetated shorelines. But one possible shortcoming was the absence of several viewers to compare results and eliminate such errors of under-representation.

Keddy (2000. P.109) identifies four parameters to quantify zonation, boundary clustering, niche width, species richness, and water level fluctuations. I elaborate on how these parameters have been taken into account in the array of available variables.

**Boundary Clustering.** Whether species distributional patterns are the result of predictable abiotic and biotic community factors, or whether it is due to stochastic causes has long been debated. But what in any case is inferred from an assembly is that the species involved had the ability to co-occur following their ecological needs. There are some cases when two species have a mutually-exclusive presence due to interspecific competition, specifically based on limiting similarity. In other words, if two species in a community setting share too many morphological and ecological features, then both species cannot occur at the same temporal and spatial scale in one shared habitat. Thus a boundary clustering is formed by them. This phenomenon is what Wiens (1989, Vol.1, p.82) refers to as “checkerboard” distribution. Based on field observations, the two groups geese and swans meet this description, and the presence of one in a micro-zone predicts the absence of the other.

**Niche width.** It is observed that if resources are distributed homogenously in a community, guild clustering does not appear, and the community lacks structural diversity. While a “patchy resource distribution” produces guild structuring. In the same way, niche width is affected by resource patchy distribution and the manner in which individuals interact for these resources forms niche partitioning patterns based on interspecific competition, eventually leading to zonation patterns. Wiens makes a related comment, that if food is an important limiting resource, “communities should be structured on the basis of how food is partitioned among co-existing species” (1989, Vol.1, p.157). It will be observed that in the case of the present study, it is not food, but vegetation structure and social behavior that has the most impact on forming community structure.

**Species richness.** Using regression models is an established tool to illustrate species diversity (for example Nur et al 1999). As mentioned earlier, this study was not
focused on single species during observations. Therefore, the concept of diversity is quantified across guilds at the habitat and micro-habitat scale. This is treated in detail in the next chapter. As will be observed, cattle grazing directly affects avian and invertebrate species richness.

**Water level fluctuations.** Surface water inundation has two types of effect on wetland structural diversity: direct change on available food supplies, and indirect change of habitat by vegetation type. He has also observed some waterfowl species favor habitats with alternating vegetative patches of varying height and density occurring with patches of open water. This is what was actually perceived in the avian response to the alternating patches of bare and reeded shoreline in the study site. Detailed analysis and discussion follows in the next chapter. As a summary, the effect of sea level fluctuations on the shorelines altered the available bare shoreline, an important factor in site attractiveness.

### 1.3. The Research Topic and Objectives

This study corresponds to what Wiens (1989, Vol.1, p.71) considers a classic approach to investigate avian habitats based on their structural configuration, how habitat resources are distributed, and the rate they are available to different members. Food resource is observed to be among the factors determining occupancy patterns (*ibid*). At the very broad scale, such occupancy patterns and identifying habitat suitability factors are of use in aiding biodiversity conservation by providing empirical evidence for best practices in reserve planning and management. However, the specific objectives of this study are as follows:

- To observe the extent and nature of grazing effect on the biotic components of the ecosystem in the study site,

- To investigate assemblage patterns of the occurring waterfowl in relation to habitat structure, specifically vegetation structure,

- To record the habitat preferences of breeding and casual waterfowl during the summer staging period, and

- To explain these preferences with reference to habitat resources, particularly to available space and food.
The initial hypotheses were:

1. Habitat preference of waterfowl is positively inclined toward grazed areas at daytime activity,

2. Vegetation structure affects habitat attractiveness, and

3. Invertebrate food supply in ungrazed sample plots is higher than in grazed plots.

As will be seen, in the course of observations, and later during the analyses, the hypotheses became more specific and detailed. Regarding the first item, it is assumed that a site is more preferred if it is more populated. The second hypothesis did not specify the direction of effect. Based on previous research, it could be deduced that vegetation structure does affect habitat attractiveness, but the direction was unknown at the beginning. Vegetation Structure refers to the vertical structural variability created by emergent aquatic plants. The third hypothesis was based on the reasoning that, even if invertebrate diversity happens to be high in grazed plots, due to the larger number of avian consumers, the ultimate amount will be comparatively low. The impact of fish predators on invertebrates was assumed to be low.
2. Previous Research

A distinction can be made between different grazing intensities. Structural homogeneity is the result of heavy grazing and structural diversity follows mild grazing intensity. Structural variations include both vertical and horizontal strata. As Duncan & d’Herbes (1982) have observed, homogenous habitat structures are not preferred by wintering waterfowl; but favored by species nesting among patches of reeds, for example Coot (*Fulica atra*). According to Tanner (1992) the effects of excessive grazing include: decrease in available plant biomass, eutrophication and bacterial contamination of water, uncontrolled dispersion of plant seeds (Reeves & Champion 2004).

As mentioned earlier, both extreme grazing and absence of grazing have been shown to leave adverse effects on waterfowl. It has been confirmed in many studies (Kantrud 1985) that the most optimum level of grazing regime to suit the widest range of biodiversity is what researchers refer to as moderate grazing. This indicates a combination of open water and vegetated water to meet the habitat needs of most waterfowl.

*Habitat Preferences of Waterfowl.* It has long been an established fact that waterfowl can be classified in their habitat preferences. Weller (1999, p.161) mentions how bird assemblages of an estuarine coastal system varied with surface inundation and water depth. Waders, as shoreline specialists, increase in number as water recedes and leaves mud flats to forage for invertebrates; while divers are attracted to deeper waters for easier mobility to forage in water. Some divers tend to avoid dense stands of emergent vegetation as accessing the nest sites become difficult and also makes them more vulnerable to predators (for example in Rogers 1964, Mihelsons 1968). Open shores are attractive to ducks (*Anas* spp), semi-covered waters with emergent plants to divers (*Aythya* spp, *Podiceps* spp), and densely-covered waters to coots (*Fulica* spp) as an approximate generalization (for example in Väänänen 2001).

Regarding vegetation structure as resource access facilitator or inhibitor, Moore et al (1984) and also Popotnik & Giuliano (2000) observed that a decrease in vegetation biomass and structure had an adverse effect on avian habitats. Supporting this finding
were two other studies by Dobkin et al (1998) and Reeves & Champion (2004) who confirmed avian abundance and species richness had an indirect correlation with cattle grazing.

At the same time, some bird species, such as Lapwing (Vanellus vanellus) prefer wide open shorelines for different activities (for example in Henderson et al 2002). Obviously these species favor the gazed and bared shorelines. Studies such as McCoy & Rodriguez 1994; Guthery & Stormer 1984; Barker 2004; and Buxton 1991 have demonstrated this fact (Reeves & Champion 2004).

Halfway between these two extremes, is the general tendency among both dabblers and divers to prefer semi-open vegetated wetlands. Kantrud (1985) refers to 17 investigations with this theme. Moreover, Hopper (1972) confirms that the plant species diversity of the shorelines contributes to dabbler brood use.

On the rationale in choosing a habitat, Lanyon & Thompson (1986) investigated site-fidelity among male passerines and found out that it is the most influential factor in decision making about choosing a habitat. Site fidelity, in turn, can be the outcome of paying a lower price to maintain a low quality site instead, in favor of the high-maintenance better-quality site. An additional factor influencing site fidelity is the familiarity advantage (ibid). Knowing the dangers and safe parts, where better food can be accessed, and so on are all advantages gained by being familiar with a site. Site fidelity needs observations over several periods of time, and unfortunately was not possible at the time this work was presented.

Aquatic Macroinvertebrates. (Hereafter abbreviated to A.M.I.) One component of this study included observation of these organisms, their abundance and biomass to investigate whether they are a limiting factor. Voights (1973) asserted their indispensable role in the diet of female ducks. In any study of waterfowl it is important to assess the aquatic communities of invertebrates because of the following: they are one the two most important direct food resources for most waterfowl, not considering seabirds; they are the bottom line of coastal and tidal ecosystems, and can have a cascading bottom-up effect on the structural and functional vitality of the ecosystem (Keddy 2000, p.356 ).
Many studies have confirmed that approximately half of the diet of dabblers and divers is composed of A.M.I., and they are even more prominent in the diet of egg-laying females and chicks due to high protein content in comparison to other food resources (Keddy 2000, p.359). It has been observed that hens change from a vegetarian diet in the wintering seasons to a high-protein and calcium diet of mostly aquatic invertebrates during the breeding season (Eldridge 1990). As recorded by Chura 1961, and Pehrsson 1979, insects emerging from larvae on water surface or on surface of emergent plants are very important food resources to newly-hatched ducklings (as cited in Sjoberg et al 2000).

A.M.I. constitute a significant component of waterfowl diet. But basing the judgment solely on food abundance is erroneous as food availability is as important as food abundance. Wiens (1989, Vol.1, p.323) believes although resource use and abundance are interrelated, in some situations this relationship can be skewed in a certain direction, undermining the other completely. Therefore, resource measurements and drawing interpretations based on those figures must be in conjunction with the feeding ecology of the concerned individual within the specific study circumstances.

Apart from their importance as food resource, A.M.I. are exact indicators of a wetland’s health. For instance, Joyner (1982) claims that they “may surpass all other measured physical and biological variables as indicators of wetland quality for breeding ducks”.

Aquatic Macrophytes. These are vascular plants, capable of photosynthesis, and occurring in the photic zone of aquatic systems. Depending on their vertical structure, aquatic plants can be divided into submersed, emergent, and free-floating (Encyclopædia Britannica 2013). The scope of the research was limited to observing the vertical, and to some extent, linear structure of emergent macrophytes. The study site was dominated by patches of Common Reed (Phragmites spp) and Cattail (Typha spp).

It is a well-known fact that submersed plants make a noticeable portion of the waterfowl diet, especially in three of the five bird groups studied in this work (for example in Brochet et al 2012, Crowder & Bristow 1988, van der Valk & Davis 1978). However, this aspect has been ignored and only the two plant species above
were focused on as they altered the habitat structure significantly into two distinct zones. These two have the tendency to become invasive and forming monocultures that affect the habitat structure drastically. The degree and nature of this influence differs among species and sites. Kantrud (1985) reviewed five studies which concluded such monocultures reduce water depth and slow down decomposition rate of detritus, both of which can adversely affect waterfowl.

On the other hand, the Common Reed is a generally good food source for the waterfowl, fish and aquatic invertebrates. It is attractive to all herbivorous consumers, with especially high protein content in the young shoots (Duncan & d’Herbes 1982). Moreover, most wetland common bird species use reedbeds for shelter, cover from predators, resting, sleeping and nesting. The Grey Heron, a regular breeder in Viikki, is recorded to favor dense reedbeds for nesting, and resting. (Hafner 1977, as cited in Duncan & d’Herbes 1982).
3. Materials and Methods

3.1. Study Site

The study was conducted during summer of 2012 in Viikki nature reserve, situated in the north-eastern urban boundaries of the metropolitan city of Helsinki, with the central coordinates 24° 56.00' East  60° 12.00' North. It is popularly known as Viikki, and will be referred to hereafter by this name. The total surface area of the reserve is 1,274 ha, and a wetland area of 508 ha, which is closed to public access during summer. It is a Natura 2000 designated area, and the protected wetland is ratified a Ramsar site (figures from BirdLife 2013).

The importance of this wetland is its being the staging site for large flocks of ducks, geese, waders and seabirds to breed in summer, and being home to regular and casual migratory birds in spring and summer, some of them with high conservation status. It is of national significance and is acknowledged as the most important nature reserve in Helsinki (Helsinki Environment Center). It was assessed an IBA site (Important Bird Area) in 2000 with the ratings B1i, B3, C3, denoting its biodiversity importance at the European scale and its un-threatened conservation status.¹

Despite the absence of major ecosystem threats and benefiting from an overall stable habitat viability, Viikki is surrounded by housing developments, farmlands and recreational parks. What makes it an interesting study site is its location in an urban setting, its patchy layout and possessing the attributes of an island habitat. At the local scale, the ecosystems in Viikki are varied and include intertidal coastal systems, riparian and old-growth mixed forests.

The adjacent farmlands consist of meadows that are cultivated during summer, and also as pasture meadows for domestic cattle with no specific grazing regime which during summers roam freely in expansive enclosure. One group of such cattle yearly use the ‘wet’ meadow surrounded by three sides enclosure, bordering the wetland reserve between May and June.

¹ B1i translates to “The site is known or thought to hold ≥ 1% of a flyway or other distinct population of a waterbird species.”; B3 as “Species with a favorable conservation status in Europe”; C3 as “Congregations of migratory species not threatened at the EU level” (BirdLife 2013).
From an ecological point of view, this is an estuarine wetland with both brackish and salt waters. The shorelines are subject to constant fluctuations of seawater level. Therefore, the expanse of emergent shorelines varies on a daily basis. This is a significant fact which will be elaborated later.

3.2. Study plots

Following Wiens (1989, Vol.1, p.48) the field approach was plot-based to gain an objective systematic insight into the habitat use and distribution patterns of waterfowl across the study area. As the conditions are averaged across the study area, bias is avoided and derived patterns will truly reflect how populations interact with their habitat features.

The target and control plots were of equal size 50×50 m, and as much as terrain conditions allowed, square in shape, with one transect line crossing lengthwise both the aquatic and the terrestrial substrate. Each transect line had to ideally be in the middle of the plot. The treatment plots consisted of vegetated waters bordering the shoreline and part of the meadows, while the control plots were covered with aquatic macrophytes, mainly Common reed, which over the course of the observation grew into full length at varying densities.

![Fig. 1. The position of the transect line in each study plot. The dividing line between the two areas is the shoreline.](image)

Following sea level fluctuations, this shoreline changed and retreated over land or advanced into the water body.

The control plots were positioned on the opposite side of the target plots. This arranged layout may seem to cause observation bias, and be a possible limitation. But based on the landscape features of the study site, the grazed part was a continuous span clearly separated with distinct edges from the ungrazed parts by fences and the water body. Care was taken in not placing the control and target plots adjacent to each other. There was a minimum 50-m distance between each two adjacent plots,
never sharing one single border and therefore Underwood’s ‘spillover’ effect (as cited in Wiens 1989, Vol.1, p.62) was completely avoided.

Fig. 2. Layout of the 10 study plots. Each hollow square represents one treatment or control plot. The left side ones are labeled ‘grazed’, where cattle were present on the small island. The right side plots are labeled as ‘ungrazed’, which cattle never accessed and were covered by aquatic plants on saturated soil.

© National Land Survey of Finland.

3.3. Invertebrate Sampling

Activity traps were preferred over sticky traps, corers, tube samplers and sweep nets for more accurate results on capturing nektonic mid-water organisms which are more important in the diet of dabblers (the community dominant group). As investigated by Hyvönen and Nummi (2000), activity traps are more efficient at capturing Corixidae, which are an important invertebrate family in the dabblers’ diet (de Szalay & Resh 1997). Moreover, the limitation of activity traps in not being able to capture rare and benthic organisms (see Henke & Batzer 2005) was not of concern to this study, since the objective was only to assess the amount of readily available food amounts to waterfowl.

The activity traps consisted of 1-liter glass jars. Plastic funnels with 2.5-cm openings were attached to the top of the jars. The traps were placed suspended by a thread attached to the vegetation or an inserted stick in the water bed, halfway between the water surface and
bedding, often at about 20-40 cm below the surface level. Every effort was made to keep the trap locations at a proximity of 50 cm from, and parallel to, the transect lines. However, there were instances where this step had to be adjusted as the water depth was significantly lower or higher to allow for the protocol to be in effect. Four traps were used in every study plot, totaling 40 traps in one round of sampling, and altogether 80 sampling specimen were collected in the 2 rounds of the observation. The traps were removed 48 hours afterwards, filtered and emptied into 200-ml containers for identification and recording purposes. The organisms were identified down to the family, and sometimes to the species level. As the scope of this study did not necessitate species identification, emphasis was put only on identifying the taxa as distinctly as possible; therefore the recorded classification only reflects family and order. The results were classified into incremental size classes of whole body length, adapted from the system proposed by Nudds and Bowlby (1984). The six size classes were: 0-2.5, 2.6-7.5, 7.6-12.5, 12.6-20, 21-40, and 41-60 mm. The biomass index was calculated by multiplying the size class mean by abundance.

3.4. Waterfowl Monitoring

Observations of avian behavior show how habitat resources, food and space, are distributed. This can be achieved by recording the location, movement, and duration of each activity. By recording the “behavioral activity budget of individuals … among habitats or microhabitats, the importance of various habitat features may be quantified” (Wiens 1989, Vol.1, p.49). In the present work, the focus was not on the amount of time; but on the location in which a particular activity occurred, as well as the abundance of individuals in each activity. Therefore activity durations were not recorded.

The monitoring protocol was adopted from (Wiens 1989, Vol.1, p.40) adjusted to the objectives of this study and to site-specific features. For instance, it was observed that at midday, the most common activity was either resting or sleeping. Therefore to avoid losing data on other activities, intervals were placed at differing times chosen at random, regardless of favorable weather conditions to waterfowl. As the investigation objective was to assess which shorelines are most preferred, for which activity and by which populations, continuous observation was not applicable. It is confirmed by Wiens (1989, Vol.1, p.48) that in studies of behavior frequency, interval sampling may be the most appropriate. In case of slow-moving, sedentary or cryptic behaviors, it has been confirmed that the length of observation is not effective
and wasting field effort and time (Fuler & Langslow 1984 cited in Wiens, ibid). In line with the conditions of the target organisms, I adopted this notion in forming the monitoring protocol. Therefore, the uniform observation of each plot for a fixed equal duration was rejected in favor of interval observation with time budgeting in proportion to the number of individuals, species diversity and variety of activities.

There were daily observations from two stationary viewing towers to record waterfowl number, activity, and location in relation to the study plots. To do so, a high-definition field spotting scope and binoculars were used. The monitoring was done at random times between 7 AM to 7 PM when the waterfowl were at the peak of their daily activities. Each session lasted for 2-3 hours depending on the number of species present and the variety of activities. Observations were not limited by a fixed allotted time and were in the form of interval sightings.

**Data Categorization.** Four major waterfowl activities are taken into consideration: foraging, preening, resting and sleeping. The other activities such as exploring, guarding, playing, etc are labeled under ‘other’ so the total number of frequencies per activity equals the total number of individuals per plot. Also based on their feeding behavior, the waterfowl are classified into five types: dabblers/divers, seabirds, waders, geese, and swans. As a check point, the total number of each type per plot was controlled to be equal to the total number of individuals per plot. Later, this matrix of 5x5 variables was analyzed with different statistical tools.

**3.5. Vegetation Observations**

It has been debated whether structural characteristics of a habitat are more important than its floristics for avian communities. (for example Lack 1933, Svärdson 1949, Wiens & Rotenbury 1981, Van Heurck 1985). Moreover, the nature of this investigation necessitated observing the structural properties of the shorelines. Hence, the plant species diversity and richness has not been taken into consideration. The most influential measured variable was vegetative linear coverage of shorelines, represented in percentage.

Vegetation structure is simplified in this paper by designating two groups, grazed plots with varying proportions of bare shoreline, and ungrazed plots with 0% of bare shoreline. Shoreline assessment was as follows:
• Daily recording of vegetation horizontal structure, the linear extent of bare shoreline in percentage ratios
• Specifying the type of bordering vegetation as reed or herb

In Viikki, the dominant plant in the wetland is Common Reed (*Phragmites spp*), and to a lesser extent Cattail (*Typha spp*). Both of them show invasiveness and by the end of the summer formed dense patches across the water body.

### 3.6 Abiotic Parameters

Wind speed, sea level and temperature were recorded for each observation. They were planned to be used as independent variables of habitat gradient to compare avian responses. However, due to detected weak correlations, it was preferred to compare the study plots against the habitat gradients of food and bare shoreline. The environmental factors above seemed to be approximately homogenous across the study site, and entering them in the regression analysis proved to be unrelated to the scope of this research. There was relevant support that “Traditionally, the emphasis in studies of bird habitats has been on features of structural configuration or physiognomy of habitats” (Wiens 1989, Vol.1, p.309)

### 3.7 Data Analysis

Two sets of analyses were conducted, one on avian assemblages and the other on A.M.I.. The latter was then integrated into the former to draw conclusions. For both sets and most charts, SPSS 20.0 was used and Excel 2010 was occasionally utilized for some charts. Two sets of independent data were used. One on habitat resource factors with two variables on invertebrate food index and bare shoreline. Another set consisted of variables on bird groups and bird activities. As discussed earlier, the data on waterfowl were classified *a priori* into 5 guilds based on foraging characteristics.

The *P* value is held significant at the conventional level of being smaller than 0.05. There are, however, instances where this axiom is ignored. In such cases, due reference and explanation is made. I followed Wiens (1989, Vol.1, p.67) in the belief that such a convention is not flexible enough to point out less frequent, but significant, relationships in the uncontrolled field conditions where probability is influenced by many more variables than controlled lab conditions. I adopted his remark that depending on the situation and the rarity of an event, even a *P*<0.15 can be reliably significant.
The variables of avian response to habitat use were not continuous. Moreover, none of the data series were normally distributed after verification by Kolmogorov–Smirnov test. A high majority of variables proved to be linearly inter-connected on preliminary scatter plots. The sample size was also relatively large. Hence, non-parametric and bivariate analysis methods were adopted. To identify how variables are related and the strength of the relationships, three tests were used: Pearson's correlation coefficient, Spearman's rho, and Kendall's tau-b (Corder & Foreman 2009, pp 4, 33). The minimum accepted significance level was 0.05 and all were two-tailed tests. The significant correlations were identified and summarized in each test (Appendix 6). It was noticed that Spearman revealed a higher number of relationships, not identified by the other two tests (Corder & Foreman 2009, p 123). Therefore, the significant correlations detected by Spearman test were ranked in order of strength, and summarized for interpretation.

Table 2. Comparison of significant cases by 3 statistical tests in deciding the most revealing test to interpret results of the 5 studied activities.

<table>
<thead>
<tr>
<th></th>
<th>Pearson</th>
<th>Kendall's Tau</th>
<th>Spearman</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of cases</td>
<td>325</td>
<td>325</td>
<td>325</td>
</tr>
<tr>
<td>Number of significant cases</td>
<td>50</td>
<td>50</td>
<td>55</td>
</tr>
<tr>
<td>Proportion of significant cases (%)</td>
<td>15.4</td>
<td>15.4</td>
<td>16.9</td>
</tr>
</tbody>
</table>
4. Results

As there were multiple data sets, and several variables involved, the material is divided into sections. To provide an overall picture of the obtained results the following remarks are useful.

- The proportion of all birds present in grazed plots was 4.3 times higher than in ungrazed plots.
- The proportion of all foragers in grazed plots was 3.1 times higher than in ungrazed plots.
- Vegetation structure was an exceptionally important factor in attracting waterfowl.
- A series of interactions among conspecifics and heterospecifics was present.

4.1. Aquatic invertebrates

After two rounds of observation, 14 taxa of macroinvertebrates were identified. They were categorized according to the size class suggested by Nudds & Bowlby (1984) and their biomass index was calculated accordingly as mentioned earlier.

![Graph showing distribution of macroinvertebrates by taxon. The y axis shows the mean biomass index.](image-url)
Diversity. The species diversity in the grazed plots was noticeably higher than in ungrazed plots. While 13 taxa were present in the grazed plots, only 9 taxa occurred in the ungrazed plots (Figure 3). In other words, species richness was 1.4 times higher in the grazed plots. The only taxon absent in the grazed plots, while occurring in the ungrazed plots was *Limnephilidae*.

Abundance. The family of *Asellidae* was the dominant taxon in both types of plots by a major difference with the next descending item, with 47% of the whole population in grazed plots, and 65% in the ungrazed plots. *Chironomidae*, with 15%, occupied the same rank and amount in both site types. The amount of *Valvatidae* was also approximately equal in both site types, with 11% and 9%. What distinguished the two site types remarkably was the amount of *Corixidae*. This invertebrate family is a favorite and important food item in the diet of most waterfowl and will be discussed later. While it composed 15% of the whole population in the grazed sites, only 3% of the ungrazed plots consisted of it. The remaining taxa, that is *Ephemeridae*, *Hydrachnidae*, and *Cladocera* were of equal frequency in both site types. Their relative abundance ranged between 1% and 3% (See Appendix 1).

*A.M.I. Food Index*. No significant correlation was found between A.M.I. and the waterfowl total abundance. This was tested through bi-variate regression analysis. Food supply is inherently not independent of predator density since there was a statistically negative correlation between the two variables. However, the strength of this relationship was too weak to be significant (Spearman’s rho coefficient -0.091). If the waterfowl were strongly dependent on the invertebrate food supply, the statistical relationship had to portray it likewise with a significant coefficient. It was hypothesized that this weak inter-dependency was due to sufficiency of invertebrates as food supply for waterfowl at the time of study. To verify this further, a visual comparison was made between food index and bird abundance (Figure 4). A classic predator-prey dynamic is present in this diagram, with the two variables interacting opposite to each other. This confirms the accuracy of measured parameters. But, once more, it was observed that in 70% of the cases food supply surpassed consumer demand. The population trend and site popularity not being influenced by food supplies will be discussed later in the section on temporal variation of density.
To gain a finer understanding of the relationship between food index and waterfowl, a series of scatter plots were prepared for each bird group. (Appendix 2) Consistently, the absence of a positive correlation in none of the cases, confirmed that bird presence is not influenced by the distribution of A.M.I.

Statistical tests also confirmed that invertebrate amount is not a limiting factor to none of the bird groups. Three bivariate tests (as explained in 3.7.) all suggested that the null hypothesis cannot be rejected, and that there is no significant correlation between A.M.I. as food index and waterfowl abundance or activity rates at the plot scale. A.M.I. abundance and diversity does not affect waterfowl micro-habitat preferences. (Appendix 3)

4.2. Shoreline Vegetation Structure

Vegetation structure proved to be the most influential factor in attracting waterfowl. Bare shoreline scored the highest rank of importance among the other habitat parameters. Habitat use was immensely affected by amount of available bare shoreline. There was a positive relationship between extent of available bare shoreline and total abundance of waterfowl. Specifically, groups Seabirds, Waders,
and Geese were more positively responsive to bare shoreline. Seabirds showed an exceptional dependency (Spearman's rho +0.944), next Waders (Spearman's rho +0.873), and then Geese (Spearman's rho +0.807). For the Dabbler-Diver group the correlation was still positive but relatively lower than the other three above, indicating their limited preference to bare shorelines in general (Spearman's rho 0.187). The Swans were the only group that showed a negative relationship to bare shoreline (Spearman's rho -0.220). This suggests a general avoidance of bare shorelines for important daily activities.

Vegetation structure also had a very strong correlation to many bird activities. Of the 24 test cases, 10 pairs of activity-group proved highly positive in dependency on bare shoreline, and comprising nearly half of all significant cases (Appendix 6).

The highest rate of dependency concerned foraging. All the population, except Dabbler-Diver group, showed a significant correlation in foraging activity to bare shoreline. In descending order, Seabirds, Waders and Geese showed a very biased inclination to foraging on bare shorelines. Respective Spearman's rho coefficients were +0.912, +0.874, +0.834. The Swan group also responded significantly in foraging on vegetated shorelines, and avoiding the bare shorelines (Spearman's rho -0.725).

The next activity which showed high sensitivity to bare shoreline was preening, representing 20% of all significant cases. Half of the bird groups depicted a positive relationship to bare shoreline. Both Seabirds and Geese showed approximately equally high interest in preening in bare shorelines. (Spearman's rho of +0.747 and +0.724).

The three remaining activities of Rest, Sleep, and ‘Other’ each comprised 20% of differing bird groups which correlated positively to bare shoreline. Seabirds favored bare shorelines for resting (Spearman's rho +0.722). Group Swans related positively to bare shoreline for sleeping (Spearman's rho +0.743). Similarly, Geese preferred bare shorelines in their ‘Other’ activities (Spearman's rho +0.663)

4.3. Avian Assemblages

_Guild Richness_. To determine the number of different taxa present, all the significant values for the total abundance of each bird group per plot was considered. Any value
greater than 1 was taken into account. The reason why the occurrence of one individual was not considered significant is that it did not represent a major habitat use activity. Such individuals were either purposefully exploring the microhabitats with no conspecific presence or were stochastically present due to curiosity, injury, etc.

The ten study plots were ranked according to the richness score (0-5) based on totals as explained above. It was observed that all the five grazed plots ranked higher than all the ungrazed plots. With this sharp distinction between the grazed and ungrazed plots, it can be inferred that the two categories of grazed and ungrazed sites correspond to respectively the highest and the lowest taxonomic richness. The mean taxonomic richness was 92% for the grazed plots, and 56% for the ungrazed ones. In other words, nearly all the present waterfowl populations made use of the grazed plots for one or more major activity on a continual basis. Whereas, the habitat use of the ungrazed plots was restricted to only a little more than half of the taxonomic groups.

Likewise a pattern of specialized habitat use can be observed among the three groups of waders, geese and swans. The waders and geese made zero use of the ungrazed shorelines, and were only concentrated in the grazed study plots. The swan group was more selective in habitat use and generally preferred the ungrazed plots. While 72% made use of the ungrazed plots, only 18% required the grazed plots for notably resting. The use of swans in the grazed plots can be even ignored because of its narrow temporal scale. This is so due to bias produced in statistics due to the presence of a pair of whooper swans (*Cygnus cygnus*) who showed site tenacity to one particular spot to rest and sleep during daytime for a fifth of the total observation sessions. The breeding swans who were constantly present on a daily basis were the mute swans (*Cygnus olor*), who were seldom observed in the grazed plots.

*Abundance.* In general, based on the sums derived from all observations, grazed plots were more populated, with more than three quarters of the total population. 81% of all observed individuals occurred in grazed plots, whereas only 19 % in ungrazed plots. The most significant activity in terms of number of involved individuals, i.e. foraging, also had the same pattern. Grazed plots were noticeably more frequented than ungrazed plots, with rates of 76 % compared to 24 % in
ungrazed shorelines. However, among the grazed plots, patch occupancy was not uniform and 3 of the plots contained 83% of the total population, while only 17% were observed in the remaining 2 plots. Knowing that all these five plots were equal in habitat features, the question why some plots remain almost unfrequented is raised.

The low density of these unused plots may indicate unoccupied patches due to site tenacity to the historically favorite sites. It should be reminded that the two unpopular sites were located between the two most popular sites and the vegetation structure in all plots was homogenous in species but not in linear density. In other words, the only factor differentiating the plots seems to be the amount of emergent bare shoreline. The relationship between bare shoreline and bird density was tested statistically. The Pearson test indicated there was a significant difference between the bare shoreline percentage and the total population number. The amount of bare shoreline correlates positively with bird frequency with a significance coefficient of 0.726 at the 0.05 level. (Figure 6)

Further to this, the correlation between bare shoreline and each bird group was tested separately (Appendix 3). Consistent patterns emerged from the comparison of coefficients. Three tests were used to compare the data, Pearson, Kendall’s Tau, and Spearman correlation. All three tests showed a positive correlation between bare shoreline and total population per plot. The obvious implication is that waterfowl assemblages in these sites showed a definite preference for bare shorelines compared to shorelines with reed beds. Specifically, the groups Seabird and Wader showed a strong direct correlation to bare shoreline in all three tests. The same was observed in
the group Goose confirmed by two tests. All three groups already mentioned showed significant relationship to total population per plot.

![Fig. 6. The effect of bare shoreline on attracting bird assemblages](image)

To show the structural abundance of bird groups separately, the relative abundances per plot were used. If niches do not overlap, and are continuous across the habitat gradient, species abundance will also be uniformly distributed, following constant interval ratios. Where the abundance pattern is more uniform, there is implication of homogenous habitat partitioning, and consequently less interspecific competition for suitable space (MacArthur 1957). Plotting the species number against their abundance reveals the nature of their distribution, how habitat space use is organized among the members, and whether the distribution is skewed or even (Verberk 2012).

To do so, the relative abundance of groups in each plot was ranked from highest to lowest. Then they were coordinated against the total population number of each plot, and two inferences could be derived. First, ignoring the sharp skew caused by the strong dominance of one group, the remainder of the lines showed a gradual downward trend. This uniform pattern suggests a lack of structural variety and the suppression of the minority groups. As seen in Figure 7, in 60% of the cases, the four bird groups are nearly equally distributed. It indicates an even number of individuals in each group. Second, the highly skewed plots represent habitat use of a generalist with high adaptability and low requirements. The following section further investigates the presence of generalists and identifies the specialists in the remaining minority group.
Dominance. The sum total abundance of each bird group throughout the course of observation formed the basis for calculating the relative abundance to recognize the dominant group. The dabblers-divers, followed by geese, and finally by seabirds were the dominant bird groups. As observed in Appendix 7, in 70% of the cases, dabblers-divers were the absolute dominant group. In only 20% of the cases, geese surpassed the former group in abundance. The seabirds cannot be considered true dominants since their occurrence superseded the others only in one case, and by a minor difference from the two following groups.

Population Density. This indicator is closely connected to the niche space concept and of resource accessibility. Negative density-dependence increases inter- and intra-specific competition among some, but not all taxa. Any application of density indicators and population regulation should be done in conjunction with a profound understanding of the biology of the concerned organisms.

In the present study, the plots were of equal known size, so measuring density was already inherent in the total abundance figures. The totals of population per plot were compared on the bar chart in Figure 5, and the following observations can be made. The populations are not normally distributed across the study plots. As remarked earlier on abundance, the density is noticeable higher in the grazed plots, indicating
less available space than in grazed plots. One logical explanation to this is the space taken by the other community taxa, the aquatic plants. The ungrazed plots provide less space due to interspecific competition by reeds, and lack of herbivorous predators with these plants in their diet requirements. However the necessity for induced disturbance and introducing such predators depends on comparing bird census along a spatial scale to detect declining rates. It can be deducted that in the absence of any population decline, the ‘highly’ populated grazed plots have not yet reached their carrying capacity, and the avian assemblages can remain as viable populations, if overall environmental conditions remain identical in the future.

**Temporal Variation in Density.** Following the sequence of observation times, the population underwent fluctuations. Observations began at the peak of the nesting period for dabblers, divers, and swans, and continued over a span of two months when chicks were recruited and semi-independent from parental care. Based on the total abundances, scatter plots were produced and were paired on the geographical plane.

However, the rate of this sufficiency was absent in 30% of the plots, which all happened to be in the grazed zone. This note explains logically the decreasing trend in two of the three grazed plots based on temporal population decline. The same pattern cannot be observed in Plot 1, which is grazed, has the highest total waterfowl abundance, is still slightly increasing in population, but is relatively lower in food supply.

The charts in Figure 8 clearly illustrate this trend. As abundance decreases in one plot, it is compensated by an increase in the geographically opposite plot. Therefore assemblages in micro-habitats changed according to habitat structure, which is driven by the search for better sites for the daily activities. Better sites can mean more preferred invertebrate food, its availability, or the advantages of the vegetation structure in accessing more shaded areas to escape the summer mid-day heat. This implication is treated in more detail in the Discussions chapter.
Fig. 8 Temporal fluctuations in waterfowl population. The x axis represents the sequential observation sessions from the beginning to the end of the study. The y axis represents total abundance. The vertical pairing is based on the approximate geographic layout of plots in relation to each other. The complementarity in population fluctuation can be clearly seen. In each pair, one plot is decreasing while the other is increasing in bird number.

**Mutual Exclusion.** Based on a Mann-Whitney U test, it was confirmed that there is a significant relationship in the co-occurrence of swans and geese. It was observed that where geese are present, swans avoid being present. Assuming that the community does not suffer from habitat resource shortage (as discussed in the following section), the only explanation for this pattern is mutual exclusion. (Diamond 1975) This exclusion is not necessarily always caused by competition over resources, and can sometimes be rooted in the innate social behavior of species. (Verberk 2012)

**4.4. Zonation of Activities**

The most significant daytime activity in this study was hypothesized to be *Foraging* and it was confirmed to be the most populated segment in terms of individuals involved at the rate of 42%. The next most observed behavior was *Resting* with an overall 30%. The remaining three activities, that is, *Preening, Other,* and *Sleep* had a total abundance of 14%, 10%, and 4% respectively. These figures are true at the study scale. For a more detailed description, some remarks need to be mentioned at the plot scale.
As seen from Figure 9, the budgeting of activities per plot is not normally distributed, nor evenly spread, and is heavily skewed toward the two behaviors of *Foraging*, and *Resting*. This was also confirmed by a Kolmogorov-Smirnov Test. Next, the plots were compared pairwise in a Mann-Whitney U test to detect significant difference in activity distribution between the two sets. It was confirmed that there was no statistically significant difference between the two series. \( U = 4, \ P = 0.076 \) . It can be inferred that the grazed and ungrazed plots have similar activity composition. There is no statistical evidence that there is a zonation involved in plot use, and that in the grazed-ungrazed pairing scale, no plot is specialized for one single activity. However, at the overall study scale, it can clearly be confirmed that Plots 1 and 5 (both grazed) are the most popular for resting.

![Fig.9. Proportion of avian activity per plot. The five activities as indicated in the legend from top to bottom are: Other, Foraging, Preening, Sleeping, Resting. The numbers on the x axis correspond to plot numbers. Plots 1-5 were grazed, 6-10 ungrazed.](image)
5. Discussion

The analyses clearly show that both grazed and ungrazed plots are favored at some time by different bird groups throughout the summer staging period. However, grazed plots have a considerably higher rate of attractiveness to birds. The grazed plots were more populated during the nesting and brooding period, whereas, later the reeded shorelines saw more visitors. While the grazed plots constantly remain popular, the ungrazed plots gain some attraction at the end of the brooding period. In very simplistic terms, the grazed plots retain the status of a grocery store, frequented by all the community inhabitants for some needed commodity throughout the period, while the ungrazed plots serve as the temporary private homes of the inhabitants, each with its own structure and limited (but essential) use. This similitude is used to indicate micro-habitat specialized use of space. Ricklefs and Miller (2000, p.103) introduce the idea of activity space, and define it as “the limited range of conditions” in which “each organism functions best”. This activity space constantly varies in time to suit the habitat requirements of individuals. The changes in activity space can have varying temporal trends, and are a natural frequent process at the microhabitat scale. This can partly explain trends in specialized use of particular habitat patches over the course of the observations.

All environmental conditions being equal, there are suitable plots that are unoccupied or unpopular. This can be caused by heterospecific attraction: community abundance is highest in plots with most allospecific suitability cues. As seen in this study, assemblages were concentrated in some plots while other seemingly suitable ones were left unused. If the reason is simply seasonal site tenacity, or annual site fidelity, then it is time for human intervention to popularize the empty sites.

The concept of activity space explains some trends in observation, but a deeper insight is gained after the correlations have also been observed in the light of heterospecific attraction in a habitat environment where neither food nor space resource is in serious shortage. Identical to the study by Elmberg et al (1997), heterospecific attraction was not among the pre-determined hypotheses of my research. I argued for it as a consequence of detecting the presence of interactions among bird groups, correlations with too much strength to be discarded.
Strong relevant evidence about the use of heterospecific attractiveness cues can be cited from a study of breeding site selection mechanism in waterfowl. (Ward et al 2010) Two sets of cues were compared, one related to habitat structure; the other related to social cues. It was concluded that the more experienced individuals relied on social cues; while the first-time breeders used habitat structure as positive indicator in site choice. Moreover, the findings of Elmberg et al (1997) about heterospecific attraction among dabblers both in natural and in experimental conditions is supportive of my discussion here. (See also their reference to 3 more articles on the same theme). Interestingly enough, they also confirmed the absence of resource limitation in the study site, although it was an oligotrophic system. A most probable generalizing implication will be heterospecific attraction among waterfowl is present where resource shortage is absent.

The opposite effect, i.e., mutual exclusion was assessed between swans and geese. It was observed that there was a negative relationship between the two as mentioned earlier. This can be explained partly by previous findings on ecomorphological traits influencing co-occurrence. It has been proved that the larger the body size difference within a bird guild, the more the possibility of co-occurrence (Põysä et al 1994, Elmberg et al 1997). The body size difference in the two groups of Swan and Goose was not considerable, and following the above postulate, they cannot co-occur in assemblages.

5.1. Trophic Cascades

Seabirds are the only bird group in this study which are solely piscivore; they are not directly affected by neither vegetation nor macroinvertebrates as food supply. However, they are linked in the trophic food web to both of these. Two trophic cascades can be considered in this respect. The top-down cascade resulted by fluctuations in seabird numbers, the negative effect they have on fish abundance, as prey, and the positive effect on macroinvertebrates, as prey of fish. Also from the bottom-up cascading effect, with the increase in abundance of macroinvertebrates, their fish predators increase too, and so will the seabird preying on fish.

Consequently there is no competition between Group Seabirds and the remaining groups over food supplies. Indeed, a positive interaction between these two can be the trophic facilitation seabirds provide to the remaining groups by removing fish.
from the system. This is consistent with what Wiens discusses about group foraging of mixed-species, and how “their interactions maybe mutualistic rather than competitive” (1989, Vol.1, p.341).

Weller (1999, p.75) discusses how common wetland birds separate a habitat patch and use it intensively for foraging to avoid competition and to increase efficiency. According to the results of the present study, most foragers are concentrated in the grazed Plots 1 and 5, while A.M.I. amounts are relatively higher in other plots. Therefore, once more habitat segregation caused by food shortage can be rejected.

A complementary explanation as to why Plot 1 (grazed, nearest to an adjacent mudflat) remains an all-time popular site despite a slight decline in invertebrate food amounts can be the presence of sufficient plant food supplies. It has been observed that removing of emergent plants encourages the growth of submerged plants due to receiving more light from the surface water (for example in Duncan & d’Herbes 1982). Petr (2000) assesses that only geese and swans feed strictly on plants, compared to all other waterfowl. Both feed on not only aquatic plants but also on terrestrial vegetation. Knowing that groups Dabbler-Diver, Geese, and Swans feed heavily on these submersed plants leaves no more doubts why Plot 1 is never abandoned. The slight rising trend in waterfowl abundance is most likely due to the young adults recruited earlier on in the study period. (Appendix 5)

As a whole, invertebrate food supply is not a limiting factor in determining bird presence in plots. This will be elaborated in the Discussion chapter. However, there was a general tendency for alternating micro-habitat use by shifting from the grazed to the ungrazed parts. It seems birds feel A.M.I. supplies beginning to decrease and shift to plots with higher levels of food supply as a regulating mechanism. This hypothetical compensatory attempt is in the form of a micro-migration from one side of the water body to approximately the opposite side where the shorelines were densely populated with aquatic fully-grown emergent plants.²

² However, I have no empirical evidence to offer for this emerging hypothesis of purposeful or accidental regulating response, and proving it requires further field observation.
5.2. Waterfowl Preferences

It was demonstrated that almost all bird groups showed a strong affinity to bare shorelines. This preference based on habitat structural features is also noted by Elmberg et al (1997), and they emphasized the higher importance of this factor compared to the food supply factor (equal importance in Mallards according to Nummi et al 2013). Also group species diversity was more evenly spread in general in the grazed plots and less monopolized by one dominant group. This can similarly correlate to habitat structural diversity. Likewise, the diversity in observed activities, suggests multiple uses of a microhabitat. It was shown earlier how there was a complementarity pattern in the temporal progression of micro-habitat use in pairs of grazed and ungrazed plots located opposite each other. This can suggest the importance of the densely-vegetated shorelines in maintaining the habitat needs of the breeding waterfowl in Viikki. However due to observation limitations, this statement is solely applicable to daytime presence during the peak period of summer activity.

The more densely populated a site, the more seabirds, geese, and waders are attracted to join the aggregation. This points out to the concept of facilitation, and that as stated by Presely (2010) “the intraspecific aggregation of individuals in a patchy environment can reduce competition among species to facilitate co-existence.” It can clearly be asserted that seabirds, geese, and waders favor sites with large assemblages to sparsely populated sites and are facilitation seekers. Ricklefs & Miller (2000) attribute aggregated distributions to three causes: social behavior, clumped resources, and offspring tendency to remain with parents. Seabirds are already well-known for their colonial behavior, especially during breeding and nesting. It has already been observed that ducks benefit from aggregating with seabirds in getting protection from predators (Väänänen 2001). The intraspecific facilitation dependency of these three groups can also be statistically confirmed in the direct pairing of their corresponding coefficients. In general, it can be said that within the specific temporal and spatial frame of this study, the meta-guild seabird-goose-wader highly favors not only the bare shorelines, but also the intraspecific co-occurrence in resource use. However, the generality of this statement and its application to other situations and species needs further examination.
Patterns of habitat use are shaped by prey availability, predator avoidance, and competitor avoidance (Morin 2011, p. 241). In the present research, daytime predation is ruled out in this respect as during the entire period of field observation, not one single instance of predation on waterfowl was recorded. Competition comes into force when resources are a limiting factor. Accepting that food and space are not in shortage at the particular time the study was conducted, the only option that remains is prey availability. It can be argued that lack of emergent vegetation in the aquatic portions of the grazed plots facilitates hunting for A.M.I. This facilitation offered by the simple vegetation structure of bare shorelines bordering waters with little amount of emergent vegetation comes at a price though. The declining trend in habitat use of one of the two most populated plots (plot 5) reflects waterfowl sensing decreasing food supplies, and gradually shifting toward the less populated plots with relatively more A.M.I. The results obtained from waterfowl distribution across the plot gradient were to some extent consistent with the three types of species-specific habitat preferences cited above.

5.3. Factors affecting A.M.I.

It was observed in a study by Hopper (1972) that subjecting flooded reed beds to moderate grazing assisted the ducks in entering the shorelines more easily and hence having access to more A.M.I. However, the evidence for this mechanical facilitation leading to a higher abundance of dabbler group, and low rates of A.M.I. is not observed in my study. Dabblers are the absolute dominant group in all the ungrazed plots, with a significant difference between them and the next abundant group. Therefore their presence can have a pivotal role in patterns of A.M.I. diversity and quantity. Nevertheless, based on observations, A.M.I. abundance is even higher in the ungrazed plots. (Figure 4) On the other hand, Logan (1975) noticed that excessive grazing to the point of complete eradication of aquatic vegetation can lead to a decrease in abundance of A.M.I. This is in line with the relatively low rates of A.M.I in the grazed plots, with amounts in ungrazed plots being 1.7 times higher.

Concerning species diversity, it is known that in general, disturbance increases diversity. It was earlier demonstrated that the diversity of A.M.I. in grazed plots is considerably higher than in ungrazed parts. (Appendix 1) However, Steinman et al
in 2003 investigated the correlation between cattle stocking and A.M.I. and found no effect on the latter’s community structure (cited by Reeves & Champion 2004).

It was observed that grazed plots offer both sufficient quantity and diversity of A.M.I. However, the absence of *Limnephilidae* needs to be noted. This family fails to be present in the grazed plots, although they are proven to be important in the diet of ring-necked duck (*Aythya collaris*) in North America. (For example in Hohman 1985). Another family, *Corixidae*, are also important in waterfowl diet (de Szalay & Resh 1997) The observations showed that grazed sites have approximately double the amount, so it can be inferred that grazed plots offer more palatable foods, and once more, one reason for waterfowl preferring them to undisturbed sites for foraging.
6. Conclusions

A general point needs to be mentioned here about the limitations of these observations in being used to predict annual trends for management purposes. Habitat characteristics change with time, for example during the nesting, breeding, and mating season habitat features may not remain the same. This supports the fact that the concept of habitat preference is not an externally-imposed hypothesis; but a perceived fact (Wiens 1989, Vol.1, p.308).

Management Implications. As it was discussed earlier both graze and ungrazed sites are favored by waterfowl at different spatial and temporal frequencies. Therefore, the best habitat landscape seems to be the mosaic layout, with patches of differing vegetation structure to produce heterogeneity for accommodating the highest number of waterfowl species. Differing vegetation structure offer micro-habitat mosaics each of which meets the needs of all species at different stages of the breeding and brooding season. This structural heterogeneity maintains species richness.

According to Keddy (2000, p.172), maintaining and increasing species diversity at local scale is more important than at the regional scale in a wetland. As a measure of productive management practices, care must be taken that specialists are not going to be replaced by exotic generalists. In this case, it is true that the group dabbler-divers are not inherently exotic; however, encouraging other groups to proliferate can be a management consideration.

As seen in this study, assemblages were concentrated in some plots while other seemingly suitable ones were left unused. If the reason is simply site tenacity, then it is time for human intervention to popularize the empty sites by applying attractiveness cues.

The avian communities in Viikki Reserve are composed of several species of migrating birds using this site during summer for breeding. Therefore, on the annual timescale and at the regional level, they are metapopulations with shifting habitats which are continents apart. At the local scale, they also fluctuate in micro-habitat use. As this study indicates, except for the omnipresent group of ducks, which are well known for being habitat generalists (for example in Pöysä et al 1994) the other
species seem to form site-specific aggregations that shift over time, indicating their specialized habitat use.

On the other hand, Desrochers (2003) makes reference to avian communities in fragmented forests and how decisions caused by behavior rules affect patterns of habitat use. He focuses on conspecific attraction in forming foraging patterns on habitat edges, and places as much emphasis on conspecific attraction as on habitat resources. Similarly, in the observed five groups, habitat specialization is not the only influencing factor in the decisions waterfowl make to be frequent a site more than other adjacent identical patches which are almost abandoned.

A different consideration concerns density dependence. As stated by Jamieson & Brooks (2004) the assertion that a population shows density dependence leads to important management policies that, if not correctly inferred, can lead to unwanted population decline of a target species. Therefore, interpreting results must be done in conjunction with the other population ecology indicators. Their designed model from Markov chain Monte Carlo methods identified three duck species that showed density dependence. Northern Pintail (*Anas acuta*), Redhead (*Aythya americana*), and Canvasback (*Aythya valisineria*). The Pintail is a common migrant, but not necessarily breeding, in Viikki (Mikkola *et al* 2004). However, generalizing the finding of this study must be done with care. If, for example, the target species of Viikki policy makers includes this species, then strategies must be implemented to avoid high population density in the habitat patches.

Nummi & Pöysä (1993) had observed varying responses to density-dependent habitat components among four common duck species. Also, Gunnarsson *et al* (2006) concluded that female adult *Anas platyrhynchos* survival was not density dependent, while it was so among the introduced ducklings. These and a handful similar previous studies are very close in setting to the abiotic and biotic conditions in Viikki and perhaps better models to follow.

*Three Suggestions for Further Research.* As these populations are significant in the EU Birds Directive, the need for a population viability analysis seems very beneficial for implementing best practices for waterfowl management, especially enhancing avian diversity. In addition, although the original finding by Elmberg *et al* (1997) restrictively specifies heterospecific attraction between only Mallard and Teals,
knowing that dabbler guilds can consist of as many as 7 congeneric species (Elmberg *et al* 1997), they can play a pivotal role in assemblage dynamics of guilds with allospecifics. Their study proved the existence of a positive heterospecific attraction between the local residents and the introduced species. Hence, a more species-focused study of waterfowl assemblages in the 3 distinct habitat types of the study site can be used in enhancing waterfowl diversity in Viikki.

The study site included two mudflats adjacent to the study plots, one on the grazed side and the other on the ungrazed side of the wetland. Both of these were usually populated with mostly small waders and specifically Grey herons (*Ardea cinerea*). A breeding colony of this last species was nearby in a wooded small island, and by the end of the breeding season, the fully-matured flock roamed the mudflat on the ungrazed part. The former are usually solitary foragers, but have been anecdotally said to become group foragers in conditions where food supplies are sufficient (Weller 1999, p.35). The inexperienced young adults also tend to forage and roost communally (Cook 1978). It was noticed that as the summer drew to a close, the Grey herons tended to aggregate more when roosting, preying and foraging. This was probably due to the saturated fish supplies, which in turn can indicate abundance of A.M.I. and the trophic integrity of the system. Weller (1995) observed Grey herons and Waders as suitable indicators of restoration success in a floodplain since fish size and density correlate to Heron population. Fish are good indicators of the abiotic landscape health. (Weller 1999, p.172). Another point about herons is that their diet consists exclusively of fish, so measuring food resources is more straightforward than measuring resources for the omnivorous dabblers. Although waterfowl counts are consistently recorded in Viikki, no previous study has yet been conducted on the community ecology of Herons, and other waders.

The present paper was an attempt to investigate and explain the role of vegetation structure in influencing waterfowl decisions in preferring a microhabitat to an adjacent one. The core causal process was based on community structure. A complementary investigation can be based on community function and energy flow to compare the results obtained. Waterfowl can be considered as product consumers who evaluate costs and benefits of a ‘purchase’, a food supply before decision-making. This decision is not necessarily always rational, similar to ‘impulse shopping’. McFarland (1985, p.442) presents a creative parallel between ethology
and economics, where physiological fitness is correlated to economic value, and spending power to fitness cost. Subsequent to justifying assemblage patterns in the light of vegetation structure and heterospecific attraction, viewing these patterns in the light of behavioral economics can be even more revealing.

* * *
References


* * *
Appendix 1

Abundance of taxa in grazed and ungrazed shorelines. The chart legend is arranged in the descending order of amount.
Appendix 2

Abundance of bird groups at the plot scale in relation to macroinvertebrate food supply. The y axis depicts the total macroinvertebrate biomass index, and the x axis is bird relative abundance. The number labels within the chart represent the plot identification number. Plots 1-5 were grazed, and 6-10 were ungrazed.
Appendix 3

Spearman Coefficient table of correlations between food index, bare shoreline, and different bird activities by group. The significant values are highlighted. The abbreviations are the same as in Appendix 4.
Appendix 4

Comparison of three statistical tests to detect significant relationships between bird groups, total population and bare shoreline.

Highlighted figures show significant values. In each cell, the top figure is the coefficient and the lower figure is the significance level of the 1-tailed test. It was observed that except in case of swan group, all entries responded positively to each other. Therefore, to avoid losing significant differences, the 1-tailed test was used instead of the 2-tailed.

The abbreviations in the column and row heads are:

- Dabbler-Diver
- Seabird
- Goose
- Wader
- Swan

### Table

| bare shoreline totalplot | D     | S     | G     | W     | Sw    | Dabbler-Diver
|--------------------------|-------|-------|-------|-------|-------|----------------
|                          | 1,000 | 847   | .175  | .877  | .623  | .766  |
|                          | .005  | .001  | .011  | .002  | .281  |       |
|                          | .176  | .200  | .198  | .024  | .210  | .009  |
|                          | .251  | .210  | .228  | .463  | .206  | .360  |
|                          | .877  | .774  | .193  | .100  | .701  | .600  |
|                          | .001  | .005  | .011  | .256  |       |       |
|                          | .623  | .788  | .024  | .701  | .460  | .000  |
|                          | .011  | .001  | .463  | .006  | .045  | .000  |
|                          | .765  | .442  | .210  | .608  | .450  | .100  |
|                          | .002  | .042  | .206  | .011  | .045  | .136  |
|                          | .153  | .045  | .300  | .171  | .000  | .283  |
|                          | .281  | .429  | .360  | .256  | .500  | .136  |

### Table

| bare shoreline totalplot | D     | S     | G     | W     | Sw    | Spearman
|--------------------------|-------|-------|-------|-------|-------|--------------
|                          | 1,000 | 844   | .877  | .697  | .323  | .200  |
|                          | .001  | .002  | .000  | .002  | .000  | .104  |
|                          | .176  | .200  | .198  | .024  | .210  | .009  |
|                          | .251  | .210  | .228  | .463  | .206  | .360  |
|                          | .877  | .774  | .193  | .100  | .701  | .600  |
|                          | .001  | .005  | .011  | .256  |       |       |
|                          | .623  | .788  | .024  | .701  | .460  | .000  |
|                          | .011  | .001  | .463  | .006  | .045  | .000  |
|                          | .765  | .442  | .210  | .608  | .450  | .100  |
|                          | .002  | .042  | .206  | .011  | .045  | .136  |
|                          | .153  | .045  | .300  | .171  | .000  | .283  |
|                          | .281  | .429  | .360  | .256  | .500  | .136  |

### Table

| bare shoreline totalplot | D     | S     | G     | W     | Sw    | Pearson
|--------------------------|-------|-------|-------|-------|-------|-------------
|                          | 1,000 | 885   | .900  | .689  | .012  | .200  |
|                          | .001  | .002  | .000  | .014  | .017  | .232  |
|                          | .176  | .200  | .198  | .024  | .210  | .009  |
|                          | .251  | .210  | .228  | .463  | .206  | .360  |
|                          | .877  | .774  | .193  | .100  | .701  | .600  |
|                          | .001  | .005  | .011  | .256  |       |       |
|                          | .623  | .788  | .024  | .701  | .460  | .000  |
|                          | .011  | .001  | .463  | .006  | .045  | .000  |
|                          | .765  | .442  | .210  | .608  | .450  | .100  |
|                          | .002  | .042  | .206  | .011  | .045  | .136  |
|                          | .153  | .045  | .300  | .171  | .000  | .283  |
|                          | .281  | .429  | .360  | .256  | .500  | .136  |
Appendix 5

Grazed

Temporal trends in waterfowl activity. The blue line shows foraging, and the red (darker shade) shows other activities. The x axis is observation sequence in time, and the y axis is total abundance. The topmost left plot is 1, the other plots are arranged counter clock wise according to identification number.
Appendix 6

Summary of the significant coefficients of the Spearman test at the 0.01 and 0.05 significance levels. The relationship strength between food index, bare shoreline, and different bird activities are sorted in descending order by coefficient. The abbreviations are the same as in Appendix 4. The weak relationships are not included here. Both conspecific and heterospecific interactions can be viewed in this list. Of a total of 38 inter- and intra-relationships, 10 involve conspecific, while 28 involve heterospecific attraction.

<table>
<thead>
<tr>
<th>Coefficient</th>
<th>Pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.994</td>
<td>S_preen, Sw_sleep</td>
</tr>
<tr>
<td>0.929</td>
<td>G_forage, G_preen</td>
</tr>
<tr>
<td>0.912</td>
<td>S_forage, S_preen</td>
</tr>
<tr>
<td>0.899</td>
<td>S_forage, bare_shoreline</td>
</tr>
<tr>
<td>0.898</td>
<td>S_forage, total, G_forage</td>
</tr>
<tr>
<td>0.893</td>
<td>S_forage, S_rest, G_other</td>
</tr>
<tr>
<td>0.874</td>
<td>S_forage, total, S_forage</td>
</tr>
<tr>
<td>0.869</td>
<td>W_forage, bare_shoreline</td>
</tr>
<tr>
<td>0.867</td>
<td>G_preen, G_rest</td>
</tr>
<tr>
<td>0.862</td>
<td>G_forage, G_rest</td>
</tr>
<tr>
<td>0.850</td>
<td>W_forage, S_sleep</td>
</tr>
<tr>
<td>0.847</td>
<td>W_forage, total, bare_shoreline</td>
</tr>
<tr>
<td>0.845</td>
<td>S_forage, G_forage</td>
</tr>
<tr>
<td>0.834</td>
<td>G_forage, bare_shoreline</td>
</tr>
<tr>
<td>0.816</td>
<td>S_forage, total, G_preen</td>
</tr>
<tr>
<td>0.810</td>
<td>G_preen, S_rest</td>
</tr>
<tr>
<td>-0.806</td>
<td>G_forage, Sw_forage</td>
</tr>
<tr>
<td>0.800</td>
<td>S_forage, S_rest</td>
</tr>
<tr>
<td>0.795</td>
<td>D_forage, D_sleep</td>
</tr>
<tr>
<td>0.788</td>
<td>D_forage, total, S_sleep</td>
</tr>
<tr>
<td>0.784</td>
<td>Sw_sleep, G_other</td>
</tr>
<tr>
<td>0.775</td>
<td>Sw_sleep, total, W_forage</td>
</tr>
<tr>
<td>0.770</td>
<td>S_preen, G_other</td>
</tr>
<tr>
<td>0.768</td>
<td>S_preen, total, G_rest</td>
</tr>
<tr>
<td>0.767</td>
<td>S_preen, W_forage</td>
</tr>
<tr>
<td>0.748</td>
<td>S_preen, Sw_preen</td>
</tr>
<tr>
<td>0.747</td>
<td>S_preen, bare_shoreline</td>
</tr>
<tr>
<td>0.743</td>
<td>Sw_sleep, bare_shoreline</td>
</tr>
<tr>
<td>0.738</td>
<td>Sw_preen, Sw_sleep</td>
</tr>
<tr>
<td>-0.725</td>
<td>Sw_forage, bare_shoreline</td>
</tr>
<tr>
<td></td>
<td>G_preen, bare_shoreline</td>
</tr>
<tr>
<td>---</td>
<td>-------------------------</td>
</tr>
<tr>
<td>724</td>
<td>G_rest, S_sleep</td>
</tr>
<tr>
<td>724</td>
<td>G_forage, S_rest</td>
</tr>
<tr>
<td>722</td>
<td>S_rest, bare_shoreline</td>
</tr>
<tr>
<td>717</td>
<td>S_forage, G_preen</td>
</tr>
<tr>
<td>712</td>
<td>Sw_forage, D_other</td>
</tr>
<tr>
<td>711</td>
<td>S_preen, S_rest</td>
</tr>
<tr>
<td>707</td>
<td>Sw_preen, G_other</td>
</tr>
<tr>
<td>702</td>
<td>S_forage, W_rest</td>
</tr>
<tr>
<td>701</td>
<td>S_rest, Sw_sleep</td>
</tr>
<tr>
<td>701</td>
<td>total, S_sleep</td>
</tr>
<tr>
<td>693</td>
<td>total, W_rest</td>
</tr>
<tr>
<td>691</td>
<td>S_forage, Sw_forage</td>
</tr>
<tr>
<td>685</td>
<td>W_forage, W_rest</td>
</tr>
<tr>
<td>683</td>
<td>Sw_forage, G_preen</td>
</tr>
<tr>
<td>683</td>
<td>D_forage, D_preen</td>
</tr>
<tr>
<td>667</td>
<td>total, Sw_forage</td>
</tr>
<tr>
<td>666</td>
<td>W_forage, Sw_forage</td>
</tr>
<tr>
<td>663</td>
<td>G_other, bare_shoreline</td>
</tr>
<tr>
<td>655</td>
<td>D_preen, G_preen</td>
</tr>
<tr>
<td>653</td>
<td>G_preen, G_other</td>
</tr>
<tr>
<td>648</td>
<td>W_forage, S_rest</td>
</tr>
<tr>
<td>643</td>
<td>G_rest, Sw_sleep</td>
</tr>
<tr>
<td>642</td>
<td>S_forage, G_other</td>
</tr>
<tr>
<td>642</td>
<td>D_other, W_other</td>
</tr>
<tr>
<td>640</td>
<td>G_preen, Sw_sleep</td>
</tr>
</tbody>
</table>
The relative abundance of each bird group in the 10 study plots as seen in the legend. The bird

groups are: Dabbler-Diver, Seabird, Goose, and Swan.
Scattered pockets of reed in the early growth stage on the ungrazed side.


Cattle grazing on the shorelines with waterfowl close by engaged in different activities.

A population of ducks wintering in the waters of Vanhankaupunginlahti, and used to human presence.

A swan nesting in mid-water among a pocket of reeds.

A group of Grey herons roosting in the ungrazed mudflat at the close of summer.

An assemblage of Coot and Swan foraging among scattered patches of emergent plants.