Breeding Site Selection and Breeding Success in Red-throated Divers (*Gavia stellata*): Implications for Wind Power Development

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Table of Contents

Abstract ................................................................................................................................. 2

Introduction .......................................................................................................................... 3

Project Aims and Questions ............................................................................................... 6

Methods ............................................................................................................................... 7

Breeding Surveys of Red-throated Divers ........................................................................ 7

Sampling of Environmental Variables ............................................................................... 7

Statistical Analysis: Environmental Variables Associated with Breeding Lakes ............. 11

Statistical Analysis: Correlates of Breeding Success .......................................................... 11

Analysis of Risk of Breeding Failure in Breeding Lakes on Holmöarna ............................ 12

Literature Review ................................................................................................................ 13

Results ................................................................................................................................ 14

Environmental Variables Associated with Breeding Lakes .............................................. 14

Environmental Correlates of Breeding Success: The Nine Selected Breeding Lakes ........ 15

Environmental Correlates of Breeding Success: All Surveyed Breeding Lakes ................. 16

Analysis of Risk of Breeding Failure in Breeding Lakes on Holmöarna ............................ 18

Literature Review ................................................................................................................ 20

Discussion ............................................................................................................................. 22

Literature Review on the Effects of Wind Power on Red-throated Divers ......................... 27

Collision Risk ....................................................................................................................... 27

Habitat Displacement .......................................................................................................... 29

Barrier Effects ...................................................................................................................... 30

The Cumulative Impact of the Proposed Wind Farm on Holmöarna ............................... 31

Knowledge Gaps of Wind Farm Effects on Red-throated Divers ......................................... 32

Conclusion ............................................................................................................................ 34

Acknowledgements ............................................................................................................. 34

References .............................................................................................................................. 35

Appendices ............................................................................................................................. 42
Abstract

Our alarming rate of resource exploitation and its consequences on the environment is fuelling an increase in sustainable energy production around the world. Wind power appears to be a particularly promising energy source relative to its environmental footprint, with the exception of potential negative effects of wind power on birds. Varying results from impact assessments around the world indicate that knowledge of both abiotic and biotic factors, as well as bird behavior and ecology, is required to assess the cumulative impact of any given wind farm on local bird communities. This study aims to assess the cumulative impact of a proposed wind farm on a threatened seabird, the red-throated diver (Gavia stellata), at one of its breeding “hotspots” in Sweden: the Holmöarna islands. Measurements of environmental variables in lakes on Holmöarna are combined with breeding surveys from 2012 to 2015 to assess which environmental variables may be associated with lakes that red-throated divers do or do not breed in, and which variables are correlated with breeding success. These results are combined with a literature review to assess the potential negative effects of the proposed wind farm on the breeding population on Holmöarna. The results show that average breeding success over the survey period was 0.35 fledged young per pair per year. No difference was found in environmental variables between lakes that divers had or had not bred in. Lake area/perimeter ratio and distance to the sea were significantly negatively correlated with breeding success, although distance to the sea was only significant for lakes with at least one successful breeding attempt during the survey period. Based on these correlations, 33 of a total 40 breeding lakes are shown to have relatively high area/perimeter ratios and long distances to the sea, which may pre-dispose divers breeding within them to low breeding success. These lakes are, therefore, identified as being at high-to-moderate risk of increased breeding failure if breeding success is further reduced as a result of external factors, including that of any negative impacts of the proposed wind farm. 31 of the 40 breeding lakes are also within 1 km of the proposed wind turbine sites, which may render red-throated divers breeding within them vulnerable to displacement as a result of wind farm-related disturbance. The literature review highlights the mechanisms that may determine the cumulative impact of the wind farm on red-throated divers in terms of collision mortality, habitat displacement, and barriers to movement. The strong sensitivity of red-throated divers to disturbance is considered to be the most likely driver of any negative effects of the wind farm. In this context, I thus argue the need for a precautionary approach to planning wind power developments in the vicinity of breeding red-throated diver populations.
Introduction

Both scientific and global communities are becoming increasingly aware of anthropogenic disturbances that are causing widespread degradation of ecosystems around the world (MEA 2005). These disturbances are typically grouped into one of four categories: habitat degradation, overexploitation, invasive species introductions, and disease (Diamond 1989), with climate change becoming increasingly recognized as a fifth major disturbance (IPCC 2014). Among many observed outcomes of these disturbances is an accelerated rate of extinction of the world’s species, with 18 – 35% of all terrestrial species expected to be extinct by 2050 (Thomas et al. 2004). Identifying the causes of, and preventing, these outcomes is problematic due to the immense diversity of life on Earth, the resulting complexity of ecosystem dynamics, and the interactions of organisms within ecosystems. As such, researchers are continuously working towards a better understanding of the environment, with the goal of uncovering information that will help us to minimize disturbance levels and develop strategies to slow the loss of biodiversity on Earth.

One major facet of global efforts to counteract the impacts of anthropogenic disturbance is the conversion from fossil fuelled energy sources to renewable energy sources. In 2013, fossil fuels constituted 86.3% of global primary energy sources (BP 2015), contributing to a huge increase in carbon emissions compared to pre-industrial levels, and a vast number of consequent effects on biodiversity (MEA 2005, IPCC 2014). Sweden is on target to become one of the world’s first fossil fuel-free states, having already exceeded their 2020 target of 49% national energy production from renewable sources according to the EU Renewable Energy Directive (Eurostat 2015). As a result, Sweden has seen a substantial increase in wind power development: from 2010 to 2015, the number of wind turbines has nearly doubled from 1,723 turbines to 3,244 turbines, with the resulting annual energy production more than tripling from 3.5 TWh to 15.6 TWh (Svensk Vindenergi 2011, Svensk Vindenergi 2015). A further 2,814 turbines have been approved for construction, and 4,046 turbine plans are currently under review (Svensk Vindenergi 2015). While this represents a significant step towards sustainable energy production, the potential for increased magnitude of any negative effects of wind power needs to be considered.

The potential negative impacts of wind farms on birds are a primary point of debate in wind power development. The impacts of wind farms on birds are generally summarized into three categories: collision mortality, habitat displacement, and barrier effects from avoidance of wind farms (Langston and Pullan 2003, Drewitt and Langston 2006, Hötker et al. 2006, Rydell et al. 2012). A well-acknowledged caveat of studies on these effects is that their cumulative impact is largely site- and species-specific (Langston and Pullan 2003, Barrios and Rodrigues 2004, Hötker et al. 2006, Rydell et al. 2012) and often becomes neglected in risk assessments due to a lack of localized, empirical data to measure it (Masden et al. 2010a, Busch and Garthe 2016). As such, there are a number of gaps in the knowledge needed to fully understand the risks of wind power development to birds. Our capacity to fill these gaps is, in turn, fundamentally
limited by our understanding of the interactions between birds and the environment at different spatial and temporal scales.

The vulnerability of seabirds to wind power developments has proved particularly difficult to study due to their wide geographic range, of which a majority is unknown to us over the oceans (Schmutz 2014). Seabirds typically exhibit slow life history strategies (LHS) characterized by a long lifespan and low reproductive rate (Erikstad et al. 1998, Schmutz 2014). This LHS is considered to render seabirds particularly vulnerable to anthropogenic disturbance, as small increases in adult mortality may significantly reduce population sizes because of the low recruitment rates of chicks into the population (Wilson et al. 2010, Schuster et al. 2015). Red-throated divers (Gavia stellata) are widely dispersed seabirds with relatively small local populations (the population estimate for Sweden is 1,300 – 1,900 breeding pairs, Eriksson 2010), which renders local populations particularly vulnerable to extinction from small increases in mortality. Red-throated divers are protected according to Annex I of the EU Birds Directive, as well as the Swedish Red List, because of population declines in conjunction with anthropogenic disturbances and a loss of breeding habitat (Eriksson 2010). Red-throated divers have also been identified in many reports as highly sensitive to disturbance from wind power developments (Garthe and Hüppop 2004, Bright et al. 2008, Desholm 2009, McGuinness et al. 2015), although few studies provide any concrete, empirical evidence of this. Of the studies that do provide this evidence, the great majority focus on the effect of offshore wind farms on wintering divers (Petersen et al. 2006, Wilson et al. 2010). However, the breeding ecology of red-throated divers implies that the effects of land-based wind farms in the vicinity of breeding sites may be just as, if not more, significant a risk for this species.

Red-throated divers breed in small lakes while feeding almost exclusively on marine fish, making an average of 11 foraging trips between the breeding lake and the sea per day per fledgling (Reimchen and Douglas 1984). As such, the energy costs of reproduction for red-throated divers are likely to be high, especially considering that their LHS requires high adult survival rates for migrating and winter periods (Rizzolo et al. 2015). In fact, observations of brood reduction by parents with two-chick broods (whereby only one chick is fed at the cost of starvation of the other) (Davis 1972, Bergman and Derksen 1977, Eberl and Picman 1993, Ball et al. 2007, Rizzolo et al. 2014) indicate that in many cases, the benefits of reproduction for red-throated divers are only marginally higher than the costs. Therefore, small changes in breeding conditions that contribute to breeding failure may be able to ‘tip the scales’, causing parent red-throated divers to abandon a nest and reallocate energy to surviving until the next breeding season (Erikstad et al. 1998). In this context, red-throated divers breeding in lakes with less favorable conditions for breeding may be at high risk of breeding failure if some disturbance, such as any potentially negative effects of a wind farm, increases the costs of reproduction.

The continuing degradation of lakes in Sweden as a result of pollution, acidification, and moss growth has led to a 50% decline in red-throated diver breeding lakes in Sweden over the last 50 years.
(Eriksson 1994); as such, Eriksson (2015) recommends that all potentially suitable red-throated diver breeding lakes remain unaffected by further anthropogenic developments. However, of the studies that look at environmental effects on red-throated diver breeding success, none shed light on whether certain environmental factors are inherent in breeding lakes in comparison to other lakes (Hötker et al. 2006). As red-throated divers typically show strong breeding site tenacity (Davis 1972, Bundy 1978, Gomersall 1986, Eberl and Picman 1993), it is possible that red-throated divers have adapted to select breeding lakes based on environmental conditions that they perceive to be associated with breeding success. Previous research suggests that sufficient emergent vegetation and open water cover are common environmental features in red-throated diver breeding lakes (Bundy 1978, Skyllberg et al. 1999), while other studies of breeding success disagree on the importance of features such as lake size (Skyllberg et al. 1999, Cromie 2002), distance to foraging sites (Gomersall 1986, Eberl and Picman 1993), and nesting on lake islands versus shorelines (Lokki and Eklöf 1984, Eriksson and Johansson 1997). Vegetation surrounding the lake may also affect breeding site selection: for example, due to natural acidification in Sweden, breeding lakes are transforming into peat mires through moss growth (Eriksson 1994, Skyllberg et al. 1999). The resulting floating moss belts that form within the lake shorelines may provide protection against predators. Identifying which environmental conditions are common to breeding lakes is essential to locate potential breeding sites and to plan where wind farms can be placed with the least impact on breeding red-throated diver populations.

The Holmöarna islands off the coast of the Västerbotten province in Sweden comprise one of few hotspots for breeding red-throated divers, representing approximately 1 – 2.5% of the Swedish breeding population (Eriksson 2010). A nature reserve was established on the southern island of Ängesön in 1980, covering 41 of 68 km² of Holmöarna, with the purpose of protecting the birdlife on the island (Länsstyrelsen Västerbotten 2008). Since its establishment, the breeding population of red-throated divers appears to have increased from 15 – 20 pairs in 1980 to 26 – 32 pairs in 2011 (Pettersson 2011). Other birds protected under the EU Birds Directive, including black-throated divers (Gavia arctica), ospreys (Pandion haliaetus), and white-tailed sea eagles (Haliaetus albicilla) also breed within the reserve (Länsstyrelsen Västerbotten 2008). Recent plans to establish a wind farm on Holmöarna have been delayed amid concerns of the potential negative consequences on the local breeding bird community (Gröna Holmön 2014). Understanding the cumulative impact of the proposed wind farm on these birds requires a comprehensive assessment of the potential impacts of the wind farm, in conjunction with an analysis of whether birds in certain breeding lakes on Holmöarna are more vulnerable to breeding failure as a result of these impacts than others.
Project Aims and Questions

This study examines the breeding ecology of red-throated divers through two perspectives: (i) the environmental variables associated with breeding sites and breeding success, and (ii) the effect of land-based wind power developments on breeding red-throated divers.

The first aim is to combine surveys of breeding red-throated divers with measurements of environmental variables in lakes on Holmöarna to answer the following questions:

1) Which environmental variables are associated with lakes that red-throated divers do/do not breed in?
2) Which environmental variables are correlated with breeding success of red-throated divers?
3) Based on the environmental variables that are correlated with low breeding success for red-throated divers, in which breeding lakes on Holmöarna are red-throated divers particularly vulnerable to increased breeding failure if breeding success is further reduced?

The second aim is to use the data on breeding sites and breeding success, in conjunction with a comprehensive literature review on the effects of wind power on red-throated divers, to evaluate the questions:

4) What effects may land-based wind power developments have on breeding red-throated divers?
5) What is the cumulative impact of the proposed wind farm on breeding red-throated divers on Holmöarna, taking into account the vulnerability of red-throated divers to breeding failure in certain breeding lakes?
Methods

Breeding Surveys of Red-throated Divers

To identify red-throated diver breeding lakes and determine breeding success, surveys of breeding red-throated divers were conducted by Christer Olsson every summer from 2012 to 2015. Survey methods were repeated each year as follows. In early May, a preliminary survey for the presence of red-throated divers was conducted at all lakes visible on a topographical map of Holmöarna of scale 1:25000. The number of individuals was recorded for all lakes where red-throated divers were present. Lakes where there was reason to believe that red-throated divers were present despite a lack of observation were revisited in the second half of May. Reasons for re-visiting included that individuals were seen flying or heard in the direction of the lake, that red-throated divers had bred in the lake in previous years, or that locals had observed red-throated divers at or near the lake earlier that year.

A second survey was conducted between June and July of each year for all lakes where the presence of red-throated divers was confirmed in the preliminary survey (Figure 1). In the second survey, individuals were observed for signs of territory establishment or breeding. An established territory was confirmed if a pair of red-throated divers was present at the lake, and breeding was confirmed if a red-throated diver was observed sitting on a nest. All lakes with confirmed territories or breeding were subsequently surveyed every 1 – 4 weeks until either successful or failed breeding could be confirmed. Successful breeding was defined as the presence of at least one fledged young (a juvenile of at least half the body size of the adult). Given that the incubation period for red-throated divers is approximately 30 days long (Bundy 1976), a breeding attempt was defined as failed if no parents or chicks were observed in the lake within 30 days of breeding being confirmed.

An overall measure of breeding success was determined for each identified breeding lake, shown as the average number of fledged chicks per pair per year during the survey period. The average for each lake was taken from the total number of years that red-throated divers were present in each lake.

Sampling of Environmental Variables

A total of 40 red-throated diver breeding lakes were identified during the breeding surveys. A subset of 11 of these lakes, along with 11 non-breeding lakes, was sampled for environmental variables to determine which variables are associated with red-throated diver breeding lakes. The sampling of environmental variables occurred from the 7th – 11th September 2015. A breeding lake was defined as a lake where the presence of a red-throated diver had been confirmed for at least one year during the breeding surveys. A non-breeding lake was defined as a lake with no confirmed presence of red-throated divers during any of the survey years. Pairs of breeding and non-breeding lakes to be sampled were pre-selected to minimize confounding environmental variation across the study site. The criteria used to select
breeding and non-breeding lakes in pairs were (1) that the lakes were within 1 kilometer (km) of the other and (2) that the lake surface areas were no less than half (or no more than double) the size of the other. While a total of 19 lake pairs (38 lakes) suited these criteria, 11 pairs were sampled based on time constraints and accessibility (Figure 1).

Lakes were accessed on foot from the nearest pathway. Nine environmental variables were sampled: lake depth, Secchi depth, height and density of emergent vegetation, proportion of emergent and floating vegetation cover, number of islands in the lake, length of the moss belt perpendicular to the lake shore, and distance from the lake shore to the forest. Six other environmental variables were obtained using Geographical Information Systems (GIS) tools on ArcMap 10.2.2. (ESRI 2014): lake surface area, lake perimeter, area/perimeter ratio, maximum lake length, lake age, and the distance from the lake to the sea.

The proportion of emergent and floating vegetation cover in each lake was estimated visually to the nearest 10%. The number of islands was also visually counted. Lake depth and Secchi depth were measured at the lake center (the central point was determined using the ‘Feature to Point’ tool on ArcMap). The lake center was accessed on foot using waders or by a fishing float tube when lakes were too deep for wading. In one lake (Hasabackstjärnen, a breeding lake) lake depth and Secchi depth were measured from an island within 5 meters (m) of the shoreline, as the lake was much deeper than anticipated and the fishing float tube was not brought to the lake. Secchi depth was measured using a Secchi disc, as a measure of how far light travels in the water column. Lake depth was measured as the depth of open water, disregarding lake-bottom sediments, as this is the area in the water column that red-throated divers may utilize. The Secchi disc was also used to measure lake depth, by measuring the length of the attached rope when the disc settled on top of the bottom sediment.

Points directly north, east, south, and west (0°, 90°, 180°, 270° from north respectively) of the lake center were used to measure emergent vegetation height and density in the lake, the length of the moss belt, and the distance from the lake shoreline to the forest (Figure 2). A compass and GPS navigator were used to confirm the location of each point along the lake shore. At each point, the length of the moss belt was measured as the perpendicular distance from the shoreline to the nearest shrub or tree. The distance to the forest was measured to the nearest tree perpendicular to the shoreline. Both measures are included in statistical analysis as there was often a belt of shrubbery between the moss belt and the forest; hence, these two variables account for all three vegetation types surrounding the lakes. Moss belt length and distance to the forest from each point was averaged for each lake. To measure emergent vegetation height and density, a 5 m transect was extended from the lake shore at each point towards the lake center (Figure 2). Emergent vegetation density was estimated using the line intercept method: by counting each separate plant that intercepted the transect between 1 and 5 m from the lake shore. Emergent vegetation height was estimated by measuring the height of the tallest individual plant that intercepted the transect at 1, 2, 3, 4, and 5 m (or within 20 centimeters of these points if no plants intercepted them) from the
Figure 1. Map of the two Holmöarna islands (Holmön and Ängesön) where breeding surveys and sampling of environmental variables took place, showing all surveyed breeding lakes (outlined in blue), of which 11 lakes were sampled for environmental variables (orange). Non-breeding lakes sampled for environmental variables are shown in brown. © Lantmäteriet, l2014/00601
Figure 2. Illustration of how height and density of emergent vegetation, moss belt length, and distance from the lake shore to the forest were measured, using lake Nordöstra Risstrandsjön as a template. ‘X’ marks the central point of the lake. The transect lengths are not to scale.

Shoreline. Height was not recorded if no plant intercepted the transect within this range. All measures of emergent vegetation height and density were averaged for each lake.

To obtain the six GIS-based environmental variables, vector maps of Holmöarna were obtained from the Swedish Agricultural University’s Geodata Extraction Tool (SLU 2015). Surface areas, perimeters, and area/perimeter ratios for each lake were obtained using the ‘Calculate Geometry’ tool in ArcMap. The distance to the sea was measured as the shortest distance between the lake center and the sea. Lake age (from the year of lake formation) was calculated to the nearest 222$^{nd}$ year, using height contour lines of 2 m resolution obtained from SLU GET, under the assumption that land rise in the region is approximately 0.9 m per 100 years due to isostatic rebound (Skyllberg et al. 1999). Maximum lake length was measured as the maximum straight length of open water within the lake.
Statistical Analysis: Environmental Variables Associated with Breeding Lakes

All statistical analysis was performed on the R software version 3.2.2 (R Core Team 2015). Differences in environmental variables between the 11 breeding and non-breeding lakes were evaluated through Principal Components Analysis (PCA) using the ‘FactoMineR’ package (Husson et al. 2015), to account for the large number of environmental variables relative to the lakes sampled. Nearest distance to the sea and lake surface area were not included as variables in this PCA, since lake pairs were chosen to have similar surface areas and geographic locations. The scores of the extracted principal components (PCs) were saved for each lake and used as substitutes for the environmental variables in the analysis. Differences in PC scores between breeding and non-breeding lakes were analyzed using paired t-tests.

Statistical Analysis: Correlates of Breeding Success

Correlates of breeding success were evaluated in two ways: (1) comparing breeding success against all 15 environmental variables, including lake surface area and nearest distance to the sea, in the subset of breeding lakes that were sampled for the variables, and (2) comparing breeding success against the six GIS-based environmental variables in all 40 identified breeding lakes. Only lakes with confirmed breeding attempts (not those with only confirmed presence or territory establishment) were included in this analysis.

Breeding was confirmed in 9 of the 11 breeding lakes selected for environmental sampling (only presence or territory establishment were confirmed in the other two); therefore, environmental variables from these nine selected breeding lakes were analyzed for correlations with breeding success. A PCA was used for this analysis, again due to the high number of environmental variables relative to sampled lakes. The resulting PC scores were used as substitutes for the environmental variables, and analyzed for correlations with breeding success through linear regression.

Of the 40 identified breeding lakes, 27 lakes had confirmed breeding attempts during the survey period, and were used to analyze correlations between the GIS-based variables and breeding success. One more lake (Vedaögertjärnen) was removed from the data as it had high leverage relative to the other lakes in the dataset. The environmental variable of lake age was omitted from the analysis, since lakes were unevenly distributed between lake age categories, and no difference in breeding success between lake age categories was evident.

Initial scatter plots (Appendix 1) indicated separate trends in environmental variables for lakes with positive breeding successes (lakes where at least one young fledged during the survey period) and lakes with breeding successes of 0: therefore, the data for the remaining 26 lakes was partitioned into two sets for analysis: (i) the full set of 26 lakes, and (ii) the 15 lakes with positive breeding successes. To compare the GIS-based variables against breeding success in the two lake sets, linear models based on combinations of the variables were constructed and compared for goodness-of-fit to the breeding data.
using second-order Akaike’s Information Criterion (AICc) scores. AICc scores replace Akaike’s Information Criterion scores in datasets where the ratio of sample size to number of variables is less than 40 (Burnham and Anderson 2002); for the data in this analysis, the ratios are 26 and 15 lakes over 5 variables (equal to ratios of 5.2 and 3). AICc scores were generated using the ‘AICcmodavg’ package (Mazerolle 2015). Pearson’s rank correlation coefficients were calculated between each of the GIS-based variables, revealing significant correlations between lake surface area, perimeter, area/perimeter ratio, and maximum lake length (Appendix 1). To avoid inflation of correlation coefficients, these variables were not combined in the constructed linear models. The full list of linear models compared for goodness-of-fit are given in Appendix 2. For each of the two lake sets, the linear model with lowest AICc score, or the best fit to the data, was used in regression analysis to assess correlations between the GIS-based variables and breeding success.

**Analysis of Risk of Breeding Failure in Breeding Lakes on Holmöarna**

Maps for analyzing the risk of breeding failure in the breeding lakes were created on ArcMap. The assessment of risk of breeding failure was done for all 40 identified breeding lakes, based on the environmental variables found to be significantly correlated with breeding success on Holmöarna. Assuming that breeding is more costly for red-throated divers in lakes with environmental conditions correlated with low breeding success; divers in these lakes were considered to be most vulnerable to breeding failure if external factors would further increase breeding costs. Three categories of risk were identified across the range of each environmental variable: low, moderate, and high risk, associated with high, mid-range, and low breeding success respectively. For instance, if increasing lake depth is significantly correlated with decreasing breeding success, and the measured depths range from 0.2 m to 0.8 m: low-risk lakes are lakes with depth 0.2 – 0.4 m, moderate-risk lakes have depth 0.4 – 0.6 m, and high-risk lakes have depths of 0.6 – 0.8 m. The final risk category for each lake was averaged from its risk categories for each environmental variable. If the average was between two risk categories, the higher-risk category was designated as the overall risk.

The abovementioned risk analysis applies to any external factors that reduce breeding success for red-throated divers on Holmöarna. For the purpose of evaluating the cumulative impact of the proposed wind farm on Holmöarna on breeding divers, the distance between proposed wind turbine sites and breeding lakes on Holmöarna was also calculated. Given that a buffer of 1 km between red-throated diver breeding lakes and wind turbines is recommended to avoid displacement of breeding divers (Eriksson 2010, SOF 2013), all breeding lakes within 1 km of a proposed wind turbine site on Holmöarna were identified.
**Literature Review**

Literature searches were conducted in Google Scholar and Web of Science – databases. Due to differences in specificity and search method, the search words were optimized to find relevant results in each database. In Google Scholar, searches were conducted with the key words “wind power*”, “wind energy*”, “wind farm*”, and “wind turbine*” combined with “Gavia stellata”, “red throated”, “loon*”, and/or “diver*”. Equivalent searches in Web of Science returned no relevant results – therefore, the key words “wind power*”, “wind energy*”, “wind farm*”, and “wind turbine*” were combined with “seabirds*”; “birds*” and “breeding*”; or “birds*” and “habitat*” to search through a wider array of publications. The abstracts and/or introductions were read for all results. Results that were unrelated to wind power or Gaviidae species, and that were not peer-reviewed publications or commissioned reports, were excluded from the review. Commissioned reports assessing specific wind farms were limited to Danish, Norwegian, and Swedish publications for relevance. Results focusing solely on mitigation methods and political implications rather than the effect of wind power on birds were excluded. Results that were not in English or Swedish and results to which I had no access were also excluded. The resulting literature set was supplemented with relevant publications from the references in the literature to complete the literature set reviewed for the effect of wind power on red-throated divers.
Results

A total of 59 confirmed breeding attempts were recorded across the 40 breeding lakes from 2012 to 2015, with an average breeding success of 0.35 fledged young per pair per year. The total fledged young on Holmöarna ranged from 9 to 13 per year, with the exception of 2012 when only 2 chicks fledged.

Successful breeding in more than one survey year was recorded in 6 of the 40 lakes. 13 of the 40 lakes had no confirmed breeding attempts from 2012 to 2015: of these lakes, only the presence of divers was confirmed in 1 lake, and only territory establishment was confirmed in 12 lakes.

Environmental Variables Associated with Breeding Lakes

Selected pairs of breeding and non-breeding lakes ranged from 3,931 km\(^2\) to 52,887 km\(^2\) in surface area (mean 16,837.1 km\(^2\), median 9,816 km\(^2\)), and from 196 m to 1,545 m distance to the sea (mean 823.2 m, median 808.5 m). During the environmental sampling period, lake depth was assessed to be 0.1 – 0.2 m lower than the average due to a recent dry period in the area (Christer Olsson, pers. comm.).

Three PCs were extracted for the 13 environmental variables measured in the selected breeding and non-breeding lakes, explaining a total of 70.37% of the variance in the data (Table 1). PC1 was mainly correlated with variables that describe physical lake characteristics and emergent vegetation cover, PC2 was mainly correlated with variables associated with vegetation (both in and surrounding lakes), and PC3 was correlated with a combination of these variables.

Table 1. Correlation coefficients for variables with PCs from the PCA of the 13 measured environmental variables. Significance by p-value is indicated by the number of asterisks after the correlation value (*= p<0.05 **= p<0.01 ***= p<0.001).

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
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<tr>
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</tr>
<tr>
<td>Maximum lake length</td>
<td>0.8163254***</td>
<td>0.238497279</td>
<td>0.45232258*</td>
</tr>
<tr>
<td>Secchi depth</td>
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<td>0.003979954</td>
<td>-0.37384320</td>
</tr>
<tr>
<td>Area/perimeter ratio</td>
<td>0.7707054***</td>
<td>0.171228478</td>
<td>0.43883572*</td>
</tr>
<tr>
<td>Lake perimeter</td>
<td>0.6844248***</td>
<td>0.302684213</td>
<td>0.42081274</td>
</tr>
<tr>
<td>% Emergent vegetation</td>
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<td>-0.091473280</td>
<td>-0.08798148</td>
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<tr>
<td>Emergent veg. density</td>
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<td>Moss belt length</td>
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<td>0.851838949***</td>
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<td>% Floating vegetation</td>
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</tbody>
</table>
Graphs of the PC loadings for each lake show no grouping of breeding or non-breeding lakes (Appendix 3). Paired t-tests indicate no significant difference in PC scores between breeding and non-breeding lakes for PC1 (t = 1.29, df = 10, p = 0.227), PC2 (t = -0.3195, df = 10, p = 0.756), or PC3 (t = -0.787, df = 10, p = 0.450). As such, the null hypothesis that there is no difference in the measured environmental variables between breeding and non-breeding lakes cannot be rejected, and the variables do not appear to be associated with either breeding or non-breeding lakes.

Boxplots of the PC scores between breeding and non-breeding lakes (Figure 3) show that non-breeding lakes appear to have a greater range of PC scores than breeding lakes. Levene’s tests (used because of a non-normal distribution of PC scores) showed no significant differences in PC score variance between breeding and non-breeding lakes for PC1 (F = 0.343, df = 1, p = 0.565), PC2 (F = 0.278, df = 1, p = 0.604) or PC3 (F = 0.439, df = 1, p = 0.515). As such, the null hypothesis of equal variances between breeding and non-breeding lakes cannot be rejected; therefore, there does not appear to be a larger range in values of the sampled environmental variables in non-breeding lakes.

![Boxplots of PC scores for breeding and non-breeding lakes extracted from the PCA of the 13 measured environmental variables.](image)

**Figure 3.** Boxplots of PC scores for breeding and non-breeding lakes extracted from the PCA of the 13 measured environmental variables.

*Environmental Correlates of Breeding Success: The Nine Selected Breeding Lakes*

Four PCs were extracted from the PCA of the 15 environmental variables sampled in lakes with confirmed breeding, explaining a total of 83.02% of variance in the data (Table 2). PC1 was correlated with many of the variables describing physical lake characteristics, while the three other PCs were correlated with one to three variables each. Two variables were not significantly correlated with any of the
PCs (emergent vegetation density, number of islands); therefore, regression analyses were also performed on these variables separately.

The subsequent regression analysis showed no significant correlations with breeding success for PC1 ($t = -1.19, r^2 = 0.169$), PC2 ($t = 0.003, r^2 = 9.23 \times 10^{-7}$), PC3 ($t = 0.419, r^2 = 0.0245$), PC4 ($t = 0.310, r^2 = 0.0135$), emergent vegetation density ($t = 0.413, r^2 = 0.0238$), or number of islands ($t = 1.10, r^2 = 0.147$) ($p > 0.1$ for all variables). The assumptions of regression analysis were checked and not violated in all cases except for PC2, which had a non-normal residual distribution that was skewed to the left (Shapiro-Wilk's test: $W = 0.828, p = 0.0421$). An exponential transformation of the data corrected this problem, but did not reveal a significant correlation between PC2 and breeding success ($t = 6.53, r^2 = 8.88 \times 10^{-8}, p > 0.1$). As such, the null hypothesis of no correlation between breeding success and environmental variables could not be rejected, and the 15 environmental variables do not appear to be correlated with breeding success in the nine lakes sampled for the variables.

Table 2. Correlation coefficients for variables with PCs in the PCA of the 15 environmental variables measured in lakes with confirmed breeding. Significance by $p$-value is indicated by the number of asterisks after the correlation value (*$= p < 0.05$ **$= p < 0.01$ ***$= p < 0.001$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum lake length</td>
<td>0.92895108***</td>
<td>0.24856047</td>
<td>0.17814066</td>
<td>0.04670852</td>
</tr>
<tr>
<td>Lake surface area</td>
<td>0.89887004***</td>
<td>0.32048473</td>
<td>0.17242663</td>
<td>0.18263436</td>
</tr>
<tr>
<td>Area/perimeter ratio</td>
<td>0.81055075**</td>
<td>0.30173400</td>
<td>0.19924434</td>
<td>0.15936514</td>
</tr>
<tr>
<td>Secchi depth</td>
<td>0.77162210**</td>
<td>-0.47822018</td>
<td>-0.06276350</td>
<td>0.15324069</td>
</tr>
<tr>
<td>Lake perimeter</td>
<td>0.75888976*</td>
<td>0.28755163</td>
<td>0.09911662</td>
<td>0.16672022</td>
</tr>
<tr>
<td>Lake depth</td>
<td>0.75152454*</td>
<td>-0.54534357</td>
<td>0.10786470</td>
<td>0.10310765</td>
</tr>
<tr>
<td>Distance to forest</td>
<td>-0.72498148*</td>
<td>-0.30426763</td>
<td>0.54826910</td>
<td>0.12442342</td>
</tr>
<tr>
<td>% Floating vegetation</td>
<td>0.01657774</td>
<td>0.80037808**</td>
<td>0.39616524</td>
<td>-0.35414984</td>
</tr>
<tr>
<td>Emergent veg. height</td>
<td>-0.12303789</td>
<td>0.75102732*</td>
<td>-0.40285165</td>
<td>0.06308460</td>
</tr>
<tr>
<td>Distance to sea</td>
<td>-0.17652022</td>
<td>0.64769197*</td>
<td>0.33495062</td>
<td>0.46107733</td>
</tr>
<tr>
<td>Moss belt length</td>
<td>-0.61785449</td>
<td>-0.36815596</td>
<td>0.66418713*</td>
<td>0.08412850</td>
</tr>
<tr>
<td>Lake age</td>
<td>-0.30392015</td>
<td>0.01164660</td>
<td>-0.74787399*</td>
<td>0.27725779</td>
</tr>
<tr>
<td>% Emergent vegetation</td>
<td>-0.43845904</td>
<td>-0.06420207</td>
<td>-0.04407999</td>
<td>0.83416365**</td>
</tr>
<tr>
<td>Emergent veg. density</td>
<td>-0.53571968</td>
<td>0.48354751</td>
<td>0.07887815</td>
<td>0.37570254</td>
</tr>
<tr>
<td>Number of islands</td>
<td>-0.56263322</td>
<td>0.39648131</td>
<td>-0.02961201</td>
<td>-0.40791416</td>
</tr>
</tbody>
</table>

Environmental Correlates of Breeding Success: All Surveyed Breeding Lakes

Of the linear models evaluated for goodness-of-fit to the breeding success data, 5 and 11 candidate models, for the full set of 26 lakes and the positive breeding set of 15 lakes respectively, had lower AICc values than the null (intercept-only) model (Table 3). The ‘Ratio’ model (area/perimeter ratio
against breeding success) and the ‘Distance + Length’ model (distance to the sea and maximum lake length against breeding success) had the lowest AICc scores for the full and positive breeding lake sets respectively, and therefore were selected as the linear models for regression analysis in each case.

Table 3. AICc scores and weights for each linear model tested for goodness-of-fit to breeding success in the full lake set and the positive breeding lake set. Descriptions of each model are given in Appendix 2. K is the number of parameters in each model. All models with lower AICc scores than the ‘intercept only’ model are in bold. The model with the lowest AICc score for each lake set is highlighted.

<table>
<thead>
<tr>
<th></th>
<th>Full set of lakes</th>
<th>“Positive breeding” set of lakes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AICc score</td>
<td>AICc weight</td>
</tr>
<tr>
<td>Ratio</td>
<td>3</td>
<td>32.79</td>
</tr>
<tr>
<td>Distance*Ratio</td>
<td>5</td>
<td>34.23</td>
</tr>
<tr>
<td>Distance + Ratio</td>
<td>4</td>
<td>35.19</td>
</tr>
<tr>
<td>Area</td>
<td>3</td>
<td>36.73</td>
</tr>
<tr>
<td>Length</td>
<td>3</td>
<td>38.33</td>
</tr>
<tr>
<td>intercept only</td>
<td>2</td>
<td>38.38</td>
</tr>
<tr>
<td>Perimeter</td>
<td>3</td>
<td>39.30</td>
</tr>
<tr>
<td>Distance + Area</td>
<td>4</td>
<td>39.34</td>
</tr>
<tr>
<td>Distance</td>
<td>3</td>
<td>40.60</td>
</tr>
<tr>
<td>Distance + Length</td>
<td>4</td>
<td>40.87</td>
</tr>
<tr>
<td>Distance*Area</td>
<td>5</td>
<td>41.06</td>
</tr>
<tr>
<td>Distance + Perimeter</td>
<td>4</td>
<td>41.88</td>
</tr>
<tr>
<td>global</td>
<td>7</td>
<td>42.48</td>
</tr>
<tr>
<td>Distance*Length</td>
<td>5</td>
<td>43.96</td>
</tr>
<tr>
<td>Distance*Perimeter</td>
<td>5</td>
<td>44.40</td>
</tr>
</tbody>
</table>

Regression analysis revealed a significant correlation between breeding success and lake area/perimeter ratio for the full lake set (t = 4.71, r² = 0.269, p = 0.00659) (Figure 4a). For the positive breeding lake set, distance to the sea was significantly correlated with breeding success (t = -3.95, r² = 0.526, p = 0.00194) (Figure 4b), while maximum lake length was not significantly correlated with breeding success (t = -1.90, p = 0.0821). The assumptions for regression analysis were checked and not violated in either case. In summary, area/perimeter ratio appears to be a predictor of overall breeding success in breeding lakes on Holmöarna, while distance to the sea appears to be a predictor of breeding success in lakes where at least one young fledged during the survey period.
Figure 4. The relationships between breeding success and lake area/perimeter ratio for all breeding lakes (Figure 4a), and distance to the sea for lakes with positive breeding success (Figure 4b).

Analysis of Risk of Breeding Failure in Breeding Lakes on Holmöarna

The results of this study indicate that breeding success on Holmöarna significantly decreases with increasing lake area/perimeter ratio, as well as distance to the sea in lakes where at least one young fledged during the survey period. Given that breeding success per lake can change over time, this analysis considered both area/perimeter ratio and distance to the sea as significant variables for breeding success in all 40 lakes. According to the assumptions of this analysis, breeding lakes on Holmöarna with high area/perimeter ratios and long distances to the sea are, therefore, most likely to be associated with high breeding costs, which may render red-throated divers breeding in these lakes the most vulnerable to breeding failure if the costs are increased by external factors. Area/perimeter ratios for the 40 breeding lakes ranged from 5 to 45; therefore, lakes were placed in the categories of low, moderate and high risk corresponding to ratios of 5 – 18, 19 – 31, and 32 – 45 respectively. Distance to the sea ranged from 160 to 1550 m; therefore, low, moderate and high risk categories corresponded to distances of 160 – 623 m, 624 – 1087 m, and 1088 – 1550 m respectively.

Based on the overall risk categories determined from the lake area/perimeter ratios and distances to the sea, 7 of the 40 breeding lakes are categorized at high risk, 26 of 40 lakes at moderate risk, and 7 of 40 lakes at low risk of increased breeding failure if breeding success if further reduced (Figure 5).
Figure 5. Map showing the level of risk of increased breeding failure for each red-throated diver breeding lake if negative external factors reduce breeding success. All breeding lakes within 1 km of a proposed wind turbine site are outlined in brown. The nature reserve is on the east side of the reserve border.

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Alarmingly, 3 of the high-risk breeding lakes are 3 of the only 6 lakes with successful breeding in more than one survey year.

During the survey period, 27% of the fledged young were bred in the 7 high-risk lakes, and 42% were bred in the 26 moderate-risk lakes. Therefore, if all breeding attempts in the 7 high-risk lakes were to fail in a given year due to external factors, average breeding success could (theoretically) drop from 0.35 to 0.26 young per breeding pair per year. If all breeding pairs at the 26 lakes at moderate risk also failed to breed, breeding success could drop further to 0.11 young per pair and year.

31 of the 40 breeding lakes on Holmöarna are within 1 km of a planned wind turbine site (Figure 5). Given that 1 km is the minimum recommended distance between breeding red-throated diver lakes and wind turbines (Eriksson 2010, SOF 2013), all breeding pairs in these 31 lakes are at risk of being displaced as a direct result of the proposed wind farm.

**Literature Review**

Literature searches in Google Scholar and Web of Knowledge—databases yielded approximately 250 unique results. Of these, 78 publications were selected for the literature review, of which 66 were found on Google Scholar, and 12 of Web of Knowledge. There was substantial overlap in the results both between search words and between databases. As such, given that Google Scholar was searched first, the number of relevant publications found on Web of Knowledge is higher than the number presented here. 40 publications were deemed to have useful information for the literature review, and 27 more publications were included in the review from reference lists of the originally selected publications. The publication topics appear to be well distributed between the major identified effects of wind farms (collision risk, habitat displacement, and barrier effects) (Table 4).
Table 4. The distribution of publication types and topics selected for review. The percentages are for the total publications used in the review, including publications supplemented from references.

<table>
<thead>
<tr>
<th>Publications selected for review</th>
<th>78</th>
</tr>
</thead>
<tbody>
<tr>
<td>Publications selected after reading</td>
<td>40</td>
</tr>
<tr>
<td>Publications supplemented from references</td>
<td>27</td>
</tr>
<tr>
<td><strong>Total publications used in review</strong></td>
<td><strong>67</strong></td>
</tr>
</tbody>
</table>

### Publication Type

<table>
<thead>
<tr>
<th>Publication Type</th>
<th>Number of Publications</th>
<th>Percentage of Total Number of Publications</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peer-reviewed article</td>
<td>42</td>
<td>67 %</td>
</tr>
<tr>
<td>“Gray” literature</td>
<td>22</td>
<td>32 %</td>
</tr>
<tr>
<td>Literature review</td>
<td>19</td>
<td>28 %</td>
</tr>
<tr>
<td>Modeling or simulation of data</td>
<td>9</td>
<td>13 %</td>
</tr>
<tr>
<td>Sensitivity analysis of birds to wind farms</td>
<td>8</td>
<td>12 %</td>
</tr>
</tbody>
</table>

### Publication Topic

<table>
<thead>
<tr>
<th>Publication Topic</th>
<th>Number of Publications</th>
<th>Percentage of Total Number of Publications</th>
</tr>
</thead>
<tbody>
<tr>
<td>Related to red-throated divers</td>
<td>30</td>
<td>45 %</td>
</tr>
<tr>
<td>Related to collision risk</td>
<td>40</td>
<td>60 %</td>
</tr>
<tr>
<td>Related to habitat displacement</td>
<td>39</td>
<td>58 %</td>
</tr>
<tr>
<td>Related to barrier effects</td>
<td>28</td>
<td>42 %</td>
</tr>
<tr>
<td>Related to mitigation of wind farm effects</td>
<td>34</td>
<td>51 %</td>
</tr>
</tbody>
</table>
Discussion

In this study, various environmental variables were assessed for associations with red-throated diver breeding lakes and breeding success. No difference in environmental variables was found between selected breeding and non-breeding lake pairs, indicating that red-throated divers may not have adapted to select breeding sites based on the studied environmental variables. Breeding success per lake was found to increase significantly with decreasing area/perimeter ratio of breeding lakes and distance to the sea. The latter relationship, however, was only found for lakes where at least one young fledged during the survey period. Based on these significant relationships and the high costs of breeding for red-throated divers, 7 of the 40 breeding lakes on Holmöarna were assessed to be at high risk of increased breeding failure if breeding costs are further increased as a result of external factors. A further 26 of the 40 lakes were assessed to be at moderate risk of increased breeding failure on this basis. 31 of the 40 breeding lakes were also found to be within 1 km of wind turbine sites for the proposed wind farm on Holmöarna.

The breeding success of 0.35 recorded in this study is similar to the previously recorded breeding success on Holmöarna of 0.33 fledged chicks per pair per year (Pettersson 2011). Some studies from other regions also show similar success rates (Bundy 1976, Bundy 1978, Bergman and Derksen 1977, Gomersall 1986), while other Swedish studies have reported somewhat higher success rates of 0.67 – 0.88 fledged chicks per pair (Dahlén 1996, Eriksson and Johansson 1997, Eriksson 2010). However, differences in red-throated diver breeding success in different regions and over time may be expected as natural fluctuations in local population sizes and reproduction rates have been recorded (Projekt-LOM 2014, Schmutz 2014). Such fluctuations may also have caused the particularly low breeding success recorded in 2012 of this study. Given that the breeding population on Holmöarna appears to have increased in the previous decade (Pettersson 2011), there is no reason to suspect that a breeding success of 0.35 is unsustainable.

The lack of difference in environmental variables between breeding and non-breeding lakes may be attributable to low statistical power: a paired t-test power analysis shows that at least 34 lake pairs would be required to achieve 80% statistical power to show a moderate difference between breeding and non-breeding lake variables. This is also the most likely reason for a lack of correlation between breeding success and the 15 environmental variables measured in the nine selected breeding lakes. In this context, a major limitation of this study was time allocated for sampling – however, future studies can build upon these results to isolate the effects of different environmental characteristics on red-throated diver breeding.

Given the value of Holmöarna as a high-quality breeding area for birds (Länsstyrelsen Västerbotten 2008), this lack of difference may also point to an overabundance of suitable breeding lakes relative to the red-throated diver breeding population. A similar study in the United States showed such an effect for the great northern diver (Gavia immer) (Radomski et al. 2014). Many of the sampled non-
breeding lakes looked remarkably similar to some breeding lakes, and may only have remained unoccupied due to the high breeding site tenacity of red-throated divers (Davis 1972, Bundy 1978, Gomersall 1986, Eberl and Picman 1993). This may also explain why the non-breeding lakes appeared to have a higher variance in environmental variables than breeding lakes. Extending this study over a longer time period, during which a larger subset of suitable lakes would be occupied in at least one breeding season, would allow for better differentiation between breeding and non-breeding lakes. Future studies could also aim to separate non-breeding lakes into classes by their appearance, ranging from seemingly unsuitable lakes with low water depth or little open water (for example Tuvtjärnen, Appendix 4.2.3) to lakes with abundant emergent vegetation as well as open water (for example Södra Skärnsögergraven, Appendix 4.2.7). For example, in the Västerbotten province, Skyllberg et al. (1999) found a significantly higher breeding success in lakes classed as mosaics of vegetation and open water than in lakes classed as bog-type mires. Different patterns of breeding success may also have been revealed if breeding lakes were partitioned between those with confirmed breeding versus those with only confirmed territory establishment, although such partitioning would require more samples for statistical power.

To my knowledge, no other studies have directly considered the effect of lake area/perimeter ratio on red-throated diver breeding success. However, area/perimeter ratios of lakes in this study were correlated with lake surface area, perimeter, and maximum lake length. Lake surface area has been significantly correlated with breeding success in previous studies (Gomersall 1968, Okill and Wanless 1990), while other studies show no such effect (Eriksson and Johansson 1997, Cromie 2002). Interestingly, Skyllberg et al. (1999) found no effect of lake size on breeding success on the coast of Västerbotten, suggesting that certain confounding variables may cause different breeding patterns between the Västerbotten coast and Holmöarna. Area/perimeter ratio may also be correlated with other environmental characteristics: for instance, lakes with longer shorelines relative to area have longer littoral zones, and thereby are able to support increased coverage and/or density of emergent vegetation. Emergent vegetation cover has been significantly related to red-throated diver breeding success (Bergman and Derksen 1977), and in the Västerbotten province as well (Skyllberg et al. 1999), potentially because lakes with more vegetation cover provide better shelter for chicks from predators and other disturbances. A different effect of emergent vegetation cover may also have been found in this study if the cover had been measured as an absolute value rather than a percentage. However, validating the hypothesis that the amount of emergent vegetation drives the association of breeding success with area/perimeter ratio requires further study into vegetation patterns in lakes on Holmöarna.

The most likely cause for an effect of distance from a breeding lake to the sea on breeding success is in the energy costs for parent red-throated divers to fly between breeding and foraging grounds (Eberl and Picman 1993, Rizzolo et al. 2015). As such, it makes sense that this relationship was significant only for lakes with overall positive breeding success, as frequent foraging flights are not necessary when
chicks fail to hatch. This may explain non-significant relationships between breeding success and distance to the sea found in other studies (Gomersall 1986, Douglas and Reimchen 1988, Eriksson 2006), including by Skyllberg et al. (1999) on the Västerbotten coast, that did not differentiate lakes by zero and positive breeding success. Another study found a significant difference in breeding success, but with significantly lower breeding success only for red-throated divers, with two-chick broods, breeding at a distance greater than 9 km from the sea (Eberl and Picman 1993). Given that, in this study, a significant effect was found over a maximum distance of only 1.535 km, there may be other strong factors that inflate the significance of distance to the sea for breeding success on Holmöarna. Such factors may affect breeding success either by increasing the energy costs of foraging flights for parent divers, or by increasing the vulnerability of chicks to mortality while parents are foraging. As for lake area/perimeter ratios, a more comprehensive analysis of the interactions between abiotic and biotic factors that influence breeding success on Holmöarna is needed to understand this effect.

Despite a high degree of variation in breeding success and environmental conditions between studies of red-throated diver breeding, the observed patterns of breeding often point to predation and other biotic influences as major drivers of hatching success (Bundy 1976, Bergman and Derksen 1977, Gomersall 1986, Skyllberg et al. 1999, Rizzolo et al. 2014). In contrast, environmental influences appear to become relevant to breeding success after the chicks have hatched (Eberl and Picman 1993). Certain biotic factors may also have a greater effect on breeding success on Holmöarna than the sampled environmental variables: for instance, many raptors also breed on the islands (Länswäskra Västerbotten 2008) and may prey on young divers. Changes in fish abundance over time also have a recognized effect on red-throated diver breeding success (Eberl and Picman 1993, Ball et al. 2007, Dillon et al. 2009, Rizzolo et al. 2014), and may cause the influence of other environmental factors on breeding success to fluctuate accordingly. Other, more long-term fluctuations in environmental conditions may also explain differences in observed breeding successes over time and in different regions. For instance, temporal changes in red-throated diver adult survival have been correlated with ocean-level oscillations in sea surface temperatures and marine prey (Dillon et al. 2009, Sandvik et al. 2005, Schmutz 2014). While the effect of such oscillations on reproduction has not been empirically studied, modeling studies indicate that reproduction is the life stage in seabirds most affected by large-scale climatic variation (Sandvik et al. 2012). Given the vulnerability of long-lived seabirds such as red-throated divers to variation in population size, and the threatened status of red-throated divers, the effect of such factors on red-throated diver breeding ecology also need to be considered in future studies of breeding success.

The analysis of lakes at risk of breeding failure presented in this study applies to any external factors that may increase the costs of breeding for red-throated divers on Holmöarna. For the purpose of evaluating the effect of the proposed wind farm on breeding divers on Holmöarna, this analysis will herein refer to the potential negative impacts of the proposed wind farm as the external factor.
The results of the risk analysis are based on a scenario where all breeding red-throated divers experience an equally reduced breeding success as a result of negative effects of the wind farm. As such, the results are probably an overestimation of the impact the wind farm would have on the breeding population on Holmöarna. Firstly, the effects of the proposed wind farm are currently undetermined, and any negative effects may influence different breeding lakes in different ways. For instance, the proposed wind farm would most likely only affect lakes that are far from the sea if parents have to increase their flight distance between foraging and breeding sites to avoid the wind farm (Masden et al. 2010b, ProjektLOM 2014). Even at such lakes, parent red-throated divers may be able to fly to other foraging sites to avoid the increase in energy needed to avoid the wind farm (Eriksson 2006). Secondly, the increased breeding failure at high-risk lakes would only have a significant effect on the red-throated diver population if breeding pairs always returned to the same breeding sites; however, given the possible overabundance of apparently suitable breeding lakes on Holmöarna, pairs are more likely to relocate to other lakes at less risk of breeding failure. Therefore, the real risk of increased breeding failure in lakes that are pre-disposed to low breeding success depends on the specific mechanisms by which the wind farm affects red-throated divers at each breeding lake on Holmöarna.

Despite these caveats, the high number of breeding lakes found to be within 1 km of the proposed wind turbine sites provides evidence of one mechanism by which the wind farm may affect breeding red-throated divers on Holmöarna. The sensitivity of red-throated divers to anthropogenic disturbance implies that breeding pairs within this distance of a wind turbine are likely to abandon their breeding attempt as a result of wind farm-related disturbance (Eriksson 2010, SOF 2013). If all the breeding lakes within 1 km of the proposed wind turbine sites are occupied, this represents a displacement of a large proportion of the breeding red-throated diver population on Holmöarna. In theory, this displacement would only temporarily affect breeding success, as displaced individuals could relocate to other suitable breeding lakes. However, other potential negative effects of the wind farm, combined with the high proportion of breeding lakes at moderate-to-high risk of reduced breeding success from such effects, may entail more significant impacts on the breeding success of red-throated divers on Holmöarna. Therefore, the effects of the proposed wind farm on Holmöarna on red-throated divers should be treated through a precautionary approach, which would require the wind farm to be planned so that breeding lakes are exposed to as little of the predicted risk as possible. This could be done, for instance, by locating wind turbines at least 1 km away from as many breeding lakes as possible.

In summary, the results of this study indicate that red-throated divers that breed in lakes with high area/perimeter ratios and long distances to the sea are potentially at risk of increased breeding failure if negatively affected by the proposed wind farm on Holmöarna. Furthermore, a large proportion of the breeding red-throated diver population may be expected to be displaced from breeding lakes within 1 km of the proposed wind turbine sites. If the lack of difference between breeding and non-breeding lakes...
found in this study is, in fact, due to a overabundance of suitable breeding lakes on Holmôarna, then divers that are displaced as a result of the wind farm may find new breeding sites elsewhere; however, predicting such an effect requires (1) a comprehensive analysis including other, more subtle environmental influences that determine the suitability of lakes for breeding, and (2) a better understanding of the cumulative impacts of wind power on red-throated divers. The following section will discuss the results of the literature review on the effects of wind power on red-throated divers in an attempt to fulfill the latter requirement.
Literature Review on the Effects of Wind Power on Red-throated Divers

The general consensus on the effects of wind power on birds, studied across many ecoregions and bird communities, is that the cumulative effects are inevitably site- and species-specific (Langston and Pullan 2003, Barrios and Rodríguez 2004, Hötker et al. 2006, Rydell et al. 2012, Everaert 2014, Marques et al. 2014). The following review highlights the main impacts, in the contexts of collision risk, habitat displacement, and barrier effects, that wind power may entail for red-throated divers.

Collision Risk

Of all the negative effects of wind power on birds, the risk for collision with wind turbines and associated infrastructure is perhaps the most quoted and well-studied (Erickson et al. 2001, Desholm 2009, Cook et al. 2011, Zimmerling et al. 2013, Marques et al. 2014). Reports show substantial variation in collision rates between wind farms, with average collision mortalities from 0 to 64 birds killed at single turbines per year, although typical collision rates are much lower (median 2.3 birds per turbine per year) (Rydell et al. 2012). These figures suggest that certain key factors that vary between wind farms or turbines may significantly influence collision risk.

One seemingly obvious link between birds and collision risk is that a high population density near a wind farm will increase the number of collision mortalities (Barrios & Rodríguez 2004, Kingsley and Whittam 2005, Everaert and Kuijken 2007, Zimmerling et al. 2013). However, this does not imply an increased collision risk at the individual level, as evidenced in cases where certain species (including red-throated divers) show disproportionate collision rates relative to population size (Barrios and Rodríguez 2004, Bevanger et al. 2009, Krijgsveld et al. 2009, Smallwood et al. 2009). Individual-level characteristics that influence whether a bird enters the airspace where collision is a possibility include the bird’s sensitivity to disturbance (Rydell et al. 2012), flight altitude (Furness et al. 2013, Johnston et al. 2014), proportion of time spent flying (Marques et al. 2014) and flight direction (May 2015). Weather conditions may alter some of these characteristics: for example, birds tend to fly at lower altitudes in headwinds than tailwinds (Krüger and Garthe 2001, Kahlert et al. 2012), where altitudes at headwinds often coincide with average turbine heights (Petersen et al. 2006, Rydell et al. 2012). Migrating birds may also be forced to descend to lower altitudes that coincide with wind farm heights as a result of strong winds (Drewitt & Langston 2006). In contrast, bad weather may also deter birds from flying near a wind farm if they perceive an increased risk of mortality as a result of weather conditions (Erickson et al. 2001, Barrios and Rodríguez 2004, Drewitt and Langston 2006, May 2015), which would reduce their risk of collision. Seasonal patterns can also influence collision risk, with studies showing that breeding birds tend to fly within wind farms and at turbine-level altitudes more often than non-breeding and migrating birds (Everaert and Kuijken 2007, Pettersson 2011).
A bird’s probability of evading collision, once in the airspace shared by a wind turbine, is initially dependent on its perception of the turbine, which, in turn, is limited by its visual acuity and other conditions influencing the visibility of the turbine. For example, “motion smear” occurs when a bird cannot perceive a fast-moving object, such as a wind turbine, at a certain distance from the object (Hodos 2003). As such, birds with poorer vision will perceive a turbine at shorter distances than those with high visual acuity, and therefore require a faster evasion response for the same probability of evading the turbine. Birds flying at night or in poor weather conditions may also perceive a wind turbine at shorter distances than others, or be less likely to evade it (Langston and Pullan 2003, Petersen et al. 2006, Everaert and Kuijken 2007, May 2015). Once the turbine is perceived, birds with high wing loading or otherwise poor maneuverability, as well as birds flying at high speeds, require more time and/or energy to evade it (Barrios and Rodríguez 2004, Drewitt and Langston 2006, Rydell et al. 2012, Marques et al. 2014, May 2015).

Although little is known about their visual acuity, red-throated divers are typically classed as seabirds with poor maneuverability (Garthe and Hüppop 2004) that fly at altitudes that coincide with wind turbines (Krüger and Garthe 2001); these individual-level characteristics may render red-throated divers vulnerable to collision if they fly near or within a wind farm.

In terms of wind farm configuration, location appears to be the primary factor contributing to particularly high collision mortalities (Erickson et al. 2001, Langston and Pullan 2003, Everaert and Kuijken 2007). Rydell et al. (2012) showed that the highest average collision rates across the northern hemisphere occur at wind farms on wetlands and coastlines (15.5 birds killed per turbine per year). Wind farms that intersect with bird flight paths or wind drafts used by soaring birds may also disproportionately increase collision risk for some species (Barrios and Rodríguez 2004, Everaert and Steinen 2007, Marques et al. 2014). Additionally, the spatial configuration of a wind farm can influence the likelihood of a bird both entering a wind farm and avoiding collision once flying within the farm (Schuster et al. 2015). Empirical assessments indicate that farms where turbines are clustered together (Smallwood and Thelander 2004, Schuster et al. 2015) or where turbines are arranged in rows (Langston and Pullan 2003, Drewitt and Langston 2006, Cook et al. 2014) deter birds from flying towards wind turbines, thereby lowering collision risk.

Cook et al. (2011) calculated that 5 – 10% of seabirds that enter an offshore wind farm are at risk for collision if they do not attempt to evade collision. For red-throated divers, this calculated risk was 6.9% (Cook et al. 2011). However, seabirds tend to show stronger avoidance responses of wind farms than other birds (Langston and Pullan 2003, Drewitt and Langston 2006, Petersen et al. 2006); therefore, only a fraction of the seabird population near a wind farm is likely to enter the wind farm. Although red-throated divers are considered to have a low evasion probability given their individual-level characteristics (Garthe and Hüppop 2004, Furness et al. 2013), the strong avoidance response exhibited by red-throated divers is probably the main reason for low observed collision rates at wind farms, regardless of population density.
(Bevanger et al. 2009, Rydell et al. 2012). For instance, in a study of 829 collision mortalities from wind farms across Europe, only one individual was identified as a red-throated diver (Hötker et al. 2006). This strong avoidance response complicates cumulative impact assessments of wind farm effects, because the actual number of collision mortalities will be much smaller than those calculated in impact assessments based on their individual-level characteristics (Desholm & Kahlert 2005, Petersen et al. 2006, Rydell et al. 2012, Furness et al. 2013). However, this does not imply a reduced negative impact of wind farms on red-throated divers: other effects, such as habitat displacement and barrier effects, may be more significant to the cumulative impact of wind power as a result of this strong avoidance response (Masden et al. 2010a, Masden et al. 2010b, Schuster et al. 2015, Busch and Garthe 2016).

Habitat Displacement

If a bird perceives the risk of disturbance associated with a habitat within a wind farm to be greater than the benefits of utilizing it, that habitat will be abandoned or avoided. Such habitat displacement may occur as a result of disturbance from wind farm construction (Meek et al. 1993, Pearce-Higgins et al. 2012) and/or operation (Christensen et al. 2006, Stewart et al. 2007, Loesch et al. 2013, Percival 2014). Indirect habitat displacement may also occur, whereby a habitat in the vicinity of a wind farm is avoided or abandoned as a result of the bird perceiving a high risk of disturbance from the nearby wind farm (May 2015). Indirect habitat displacement, however, is more difficult to identify as displacement from a given area may also be attributed to natural temporal variation or other disturbances (Topping and Petersen 2011, Niemuth et al. 2013).

Overall, the extent of the area that is abandoned/avoided appears to be site- and species-specific, with studies showing conflicting effects on different species in one wind farm site (Pearce-Higgins et al. 2009, Niemuth et al. 2013) and between individuals of a species in different sites (Guillemette and Larsen 2002, Nilsson 2012). In contrast, some cases also show an increase in habitat quality associated with a wind farm, for example through wind farm infrastructure acting as perches for foragers (Langston and Pullan 2003, Dierschke and Garthe 2006, Petersen et al. 2006, Smallwood et al. 2009) or from a more abundant prey community forming within a wind farm site (Anderson et al. 2007). In general, birds identified as the most sensitive to anthropogenic disturbance, including many seabirds, appear to be displaced from habitats within a larger range of wind farms than other birds (Langston and Pullan 2003, Dierschke and Garthe 2006, Larsen and Guillemette 2007, Rydell et al. 2012). At offshore wind farms, seabirds have been observed to avoid habitats up to 2 – 4 km from wind farm sites (Petersen et al. 2006, Eriksson 2009). Even among seabirds, red-throated divers are especially sensitive to anthropogenic disturbance, as observed in wind farm impact assessments (Christensen et al. 2006, Petersen et al. 2006, Halley and Hopshaug 2007, Percival 2014, Petersen et al. 2014) and through sensitivity analyses from sites across Europe (Garthe and Hüppop 2004, Bright et al. 2008, Desholm 2009, Furness et al. 2013, Bradbury et
Breeding birds generally appear to be displaced over shorter distances than their non-breeding counterparts (Drewitt & Langston 2006, Hötker et al. 2006), although in species with high breeding site tenacity, the displacement of breeding populations may be a latent effect that arises as new breeders are recruited into the population (Drewitt and Langston 2006, Masden et al. 2010a). Breeding red-throated divers have been observed to abandon nests as a result of other anthropogenic disturbance (Johnson and Johnson 1935, Norberg and Norberg 1971, Bergman and Derksen 1977, Gomersall 1986, Rizzolo et al. 2014, McGuiness et al. 2015), indicating that breeding red-throated divers may also be vulnerable to habitat displacement as a result of wind farms. Post-construction studies at the Smøla wind farm in Norway indicated that breeding red-throated divers had been displaced up to 2 km from the wind farm perimeter (Halley and Hopshaug 2007). Furthermore, displaced red-throated diver populations have shown little evidence of returning to such areas, unlike some other seabirds that appear to habituate to the presence of wind farms (Halley and Hopshaug 2007, Leonhard et al. 2013, Percival 2014).

Reports from offshore wind farms suggest that habitat displacement for overwintering seabirds will have a negligible effect on seabird populations, as the seas provide an abundance of high-quality habitat (Petersen et al. 2006, Nilsson 2012, Furness et al. 2013, Petersen et al. 2014). Topping and Petersen (2011) suggest that even high concentrations of offshore wind farms in the Baltic Sea would result in a less than 2% reduction in red-throated diver population size. However, if high-quality habitats are in short supply, due to the habitat being rare, degraded, or already in use by conspecifics, a population may reduce in size as a result of such displacement (Masden et al. 2010a, Rydell et al. 2012, Cook et al. 2014, Schuster et al. 2015). Given their relatively specific breeding habitat requirements (Garthe and Hüppop 2004) and naturally low reproductive rates (Erikstad et al. 1998), red-throated divers are at risk for population decline given displacement. This, coupled with the considerable probability that red-throated divers will abandon breeding habitats within and near a wind farm, makes habitat loss by displacement the primary factor to consider in assessing the cumulative impacts of wind farms on red-throated divers.

**Barrier Effects**

Barrier effects refer to the active, in-flight avoidance of a wind farm, which typically increases the energy costs of flying as the flight distance around the wind farm increases (Hötker et al. 2006). Seabirds are often subject to barrier effects given their strong avoidance responses: for example, Petersen et al. (2006) showed that 71 – 86% of all seabirds avoided flying within 1.5 – 2 km of Danish offshore wind farms, with maximum avoidance distances at 5 km. For red-throated divers, maximum avoidance distances of 5 – 6 km have been recorded (Petersen et al. 2014). Calculations of energy
expenditure indicate that the increased energy cost of avoiding a wind farm during flight is typically negligible: for example, increased energy costs of 0.2 – 0.7% have been calculated for migrating Eider ducks passing offshore wind farms in Denmark (Petersen et al. 2006) and Sweden (Pettersson 2005). Low costs have been calculated for other migrating seabirds as well (Desholm & Kahlert 2005, Christensen et al. 2006, Masden et al. 2012), including red-throated divers (Pettersson 2011). However, the cumulative energy cost from avoidance over multiple flights may have significant impacts on individual fitness (Masden et al. 2010b). Given that red-throated divers fly to foraging grounds an average of 11 times per day to feed a single chick during the pre-fledging period (Reimchen and Douglas 1984), wind farms located between breeding and foraging sites may significantly increase the energy cost of reproduction for breeding red-throated divers (Masden et al. 2010b, Projekt-LOM 2014, Schuster et al. 2015). If combined with extraneous factors such as a low abundance of foraging sites, low food abundance or poor weather conditions, the cumulative impact of such barrier effects may cause breeding failure and reduce the red-throated diver population size over time (Masden et al. 2010b).

The Cumulative Impact of the Proposed Wind Farm on Holmöarna

In preparation for the proposed wind farm on Holmöarna, Pettersson (2011) conducted a risk assessment of how divers and white-tailed sea eagles on Holmöarna would be affected by the wind farm. Using observations of flight direction and altitude, Pettersson (2011) calculated that an average 0.5 – 1 red-throated diver individuals would be at risk of colliding with the planned wind turbines per year, which could increase annual mortality on Holmöarna from the natural rate of 5% to 6.67%. Pettersson (2011) concluded that the effects of the planned wind farm on the breeding population would be negligible, given that (1) no foraging flight paths crossed the planned turbine sites, (2) no wind turbines would be situated within 250 m of known breeding lakes, and (3) any displaced red-throated divers may choose a new breeding site within the nature reserve on the southern island of Ängesön, thereby increasing its value for conservation. In light of the empirical results and the literature review presented in this study, a number of potential limitations of this assessment can be discussed. Firstly, the low probability of collision mortality calculated by Pettersson (2011) cannot be used to justify a low impact of the wind farm on red-throated divers, since red-throated divers show strong avoidance responses to wind farms (Petersen et al. 2006, Halley and Hopshaug 2007, Percival 2014). Rather, any negative impacts of avoidance are more likely to determine the cumulative effect of the proposed wind farm than collision risk. Secondly, Pettersson’s (2011) proposed buffer of 250 m between breeding lakes and wind turbines falls far short of the 1 km buffer that is recommended to avoid habitat displacement of breeding red-throated divers (Bright et al. 2008, Eriksson 2009, SOF 2013). Thirdly, the assumption that displaced pairs may relocate to the reserve is as yet unjustified, since other unknown environmental factors may render lakes within the reserve
unsuitable for breeding. This is supported by the fact that a majority of breeding red-throated divers, both in this study and in Pettersson (2011), bred outside of the reserve.

The information presented in this literature review, combined with the analysis of risk associated with the proposed wind farm on the basis of environmental correlates of breeding success, suggest that the cumulative impacts of a wind farm could have a significant effect on red-throated diver breeding success on Holmöarna. Overall, the main driver of these effects appears to be habitat displacement as a result of a high sensitivity to anthropogenic disturbance. That said, the focus of this review has been on the full range of potential risks of a wind farm to breeding red-throated divers – in reality, many of the identified risks may not occur or may be reduced. To identify which risks are more likely to be realized, however, requires a substantial amount of research that has yet to be undertaken.

*Knowledge Gaps of Wind Farm Effects on Red-throated Divers*

The majority of relevant publications on the effects of wind power on red-throated divers focus on wintering populations at offshore wind farms, as they spend a majority of their lives at sea and are less dispersed in overwintering grounds than when breeding (Wilson *et al.* 2010). Only one, non-peer-reviewed, publication gives empirical evidence of wind farm effects on breeding red-throated divers (Halley and Hopshaug 2007). The small global population size of red-throated divers relative to their distribution also implies that a high survey effort is required for sufficient statistical power in empirical studies (Radomski *et al.* 2014). As such, the conclusions made on the effects of wind power on breeding red-throated divers are mostly speculative, and should be interpreted as such. The results of the available literature also need to be interpreted with precaution: for example, Ferrer *et al.* (2012) show that pre-construction estimates of collision risk are rarely consistent with real, post-construction collision rates, suggesting that the cumulative effects of collision risk factors are not being considered. Other reviews highlight that available studies provide poor evidence for assessing overall impacts of wind farms on birds, given the high variation in both species- and site-specific results and the inconsistent methodology between studies assessing them (Fox *et al.* 2006, Stewart *et al.* 2007). A lack of long-term studies further limits our ability to assess the cumulative impacts of a given wind farm over time, especially with regards to red-throated divers and other seabirds with relatively large, long-term natural fluctuations in population size and breeding success (Projekt-LOM 2014, Rizzolo *et al.* 2014, Schmutz 2014). These impacts also need to be considered on larger spatial scales: for instance, while single assessments of offshore wind farms consider the effects of habitat displacement on overwintering red-throated divers to be negligible (Petersen *et al.* 2006, Nilsson 2012), Busch *et al.* (2013) show that the cumulative displacement effects from offshore wind farms in the UK, Netherlands, Belgium and Germany corresponds to a 5.42% loss of red-throated diver wintering habitat.
To minimize the potential effects of wind power on birds, risk assessments are integrating strategies such as spatial sensitivity maps (Bright et al. 2008, van Haaren and Fthenakis 2011, Winiarski et al. 2014, Christel et al. 2015), more accurate remote sensing technologies (Desholm and Kahlert 2005, Drewitt and Langston 2006), and controls of both pre- and post-construction effects (Bevanger et al. 2009, Masden et al. 2010a) to better identify and avoid the negative effects of wind power. Post-construction mitigation methods are also being implemented, including measures such as increasing the visibility of turbines to birds (Drewitt and Langston 2006) and shutting turbines off during periods with high risk of collision (de Lucas et al. 2012, Singh et al. 2015). In the case of red-throated divers, there is no evidence of habituation to the presence of wind farms (Leonhard et al. 2013, Percival 2014); therefore, pre-construction mitigation of wind farm effects appears to be necessary. This study demonstrates that a large number of red-throated diver breeding lakes on Holmőarna are vulnerable to disturbance from the proposed wind farm, both because many lakes are within 1 km of the wind turbine sites, and because of environmental variables that pre-dispose certain breeding lakes to yielding low breeding success. Whether the proposed wind farm contributes to breeding failure in lakes with low breeding success depends on the mechanisms by which the wind farm affects red-throated divers: for example, a wind turbine placed between breeding and foraging grounds may force parent red-throated divers to take longer flight routes to forage for their chicks (Masden et al. 2010b). To assess the potency of this risk requires the identification of (1) foraging sites around Holmőarna and how their distribution may change over time, (2) flight paths from each breeding lake to foraging sites, and (3) other indirect effects of wind farms on breeding red-throated divers, for instance through the displacement of predators or conspecifics, which may increase competition or predation for breeding divers.
Conclusion

The aims of this study were to identify environmental variables that are associated with red-throated diver breeding lakes and breeding success, the results of which were combined with a literature review to assess the potential cumulative effects of a proposed wind farm on Holmöarna on the breeding red-throated diver population. Given that lakes with the highest area/perimeter ratios and distances to the sea were associated with the lowest breeding success (the latter only in lakes where successful breeding attempts had occurred), a majority of breeding lakes on Holmöarna were found to be at moderate to high risk of increased breeding failure if breeding success was further reduced by external factors, including that of any negative effects of the proposed wind farm. A majority of lakes were also located within 1 km of the proposed wind turbine sites, rendering breeding pairs within them vulnerable to displacement due to their high sensitivity to anthropogenic disturbances. Based on the literature reviewed in this study, the main negative effects of a wind farm on breeding red-throated divers include habitat displacement as a result of wind farm-associated disturbance, and the increased energy costs of avoiding the wind farm if wind turbines are situated between breeding and foraging grounds. Further empirical evaluations of the potency of these effects on Holmöarna are required, as the negative effects identified in this study represent the full array of possible effects, rather than those most likely to occur. Although the lack of difference found between breeding and non-breeding lakes may indicate that there is an abundance of suitable breeding lakes for affected divers to relocate to, a better understanding of the environmental conditions that constitute suitable breeding sites is necessary to provide evidence to support this hypothesis. Given the number of unknowns in the site-specific, cumulative impacts of the proposed wind farm, and the threatened state of red-throated divers in Sweden, a precautionary approach in wind power development is necessary to minimize any potential for negative impacts of wind farms on breeding red-throated divers. Such an approach may allow red-throated diver populations to be sustained until we acquire the knowledge needed to conserve diverse bird communities in conjunction with the management of wind power and other environmental resources.

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Appendices

Appendix 1. Plots of red-throated diver breeding success in the 27 lakes with confirmed breeding during the survey period against the six GIS-based variables: lake surface area, area/perimeter ratio, lake perimeter, nearest distance to the sea, maximum lake length, and lake age.
**Appendix 2.** List of the linear models included in model selection for regression analyses of red-throated diver breeding success against the five GIS-based variables.

<table>
<thead>
<tr>
<th>Model Abbreviation</th>
<th>Model Parameters</th>
<th>Number of Parameters</th>
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<td>Area</td>
<td>Area only</td>
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<tr>
<td>Perimeter</td>
<td>Perimeter only</td>
<td>3</td>
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<tr>
<td>Ratio</td>
<td>Area/perimeter ratio only</td>
<td>3</td>
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<tr>
<td>Length</td>
<td>Maximum lake length only</td>
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<tr>
<td>Distance</td>
<td>Distance to the sea only</td>
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<td>Distance + Area</td>
<td>Distance to the sea + area</td>
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<tr>
<td>Distance + Perimeter</td>
<td>Distance to the sea + perimeter</td>
<td>4</td>
</tr>
<tr>
<td>Distance + Ratio</td>
<td>Distance to the sea + area/perimeter ratio</td>
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<tr>
<td>Distance + Length</td>
<td>Distance to the sea + maximum lake length</td>
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<tr>
<td>Distance*Perimeter</td>
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<tr>
<td>Distance*Length</td>
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<td>Area + perimeter + area/perimeter ratio + maximum lake length + distance to the sea</td>
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</tr>
</tbody>
</table>
Appendix 3. Graphs of Principal Component (PC) loadings of lakes used in the analysis of environmental variables associated with breeding and non-breeding lakes.

3.1 PC loadings of breeding and non-breeding lakes for PC1 and PC2

3.2 PC loadings of breeding and non-breeding lakes for PC1 and PC3
3.3 PC loadings of breeding and non-breeding lakes for PC2 and PC3
Appendix 4. Names, coordinates, surface areas, and images of each lake that was selected for analysis of environmental differences between breeding and non-breeding lakes. Lake coordinates are given in the SWEREF TM geographic coordinate system.

4.1 Lakes that red-throated divers have been observed in (breeding lakes), ordered by surface area.

4.1.1 Nordöstra (NO) Risstrandsjön (X 790519, Y 7086492); 4,060 m²

4.1.2 Hamntutterdiket (X 789105, Y 7082895); 5,280 m²
4.1.3 Hasabackstjärnen (X 788136, Y 7085815); 7,193 m²

4.1.4 Västra Flaggdiket (X 787729, Y 7086179); 7,879 m²

4.1.5 Abborrkrokgraven (X 791256, Y 7079226); 10,250 m²
4.1.6 Sör Skatasjön (X 789572, Y 7082583); 10,576 m²

4.1.7 Skärnäsögergraven (X 791190, Y 7081942); 11,437 m²

4.1.8 Lill Kvistersviken (X 791117, Y 7085928); 12,513 m²
4.1.9 Kopptjärnarna (X 791762, Y 7079233); 22,934 m²

4.1.10 Lill Fanasjön (X 790074, Y 7087378); 29,170 m²

4.1.11 Halörsgreven (X 791392, Y 7077028); 52,887 m²
4.2 Lakes that red-throated divers have not been observed in (non-breeding lakes), ordered by corresponding lake pairs in 4.1 (Lakes 4.1.1 and 4.2.1 were paired breeding and non-breeding lakes, etc.).

4.2.1 Stenicken (X 790406, Y 7086410); 4,206 m²

4.2.2 Mellersta Skatasjön (X 789437, Y 7082668); 3,931 m²

4.2.3 Tuvtjärnen (X 787868, Y 7085636); 8,195 m²
4.2.4 Sör Jonasdiket (X 787578, Y 7085797); 7,658 m²

4.2.5 Lill Långskärsgaven (X 791227, Y 7078966); 6,483 m²

4.2.6 Måsgrundgraven (X 789806, Y 7082857); 11,029 m²
4.2.7 Södra Skärnäsögergraven (X 791395, Y 7081476); 9,067 m$^2$

4.2.8 Västra Jönskärsdiket (X 791417, Y 7085879); 9,382 m$^2$

4.2.9 Långklintgraven (X 791924, Y 7078675); 38,326 m$^2$
4.2.10 Stor Fanasjön (X 790304, Y 7087131); 45,093 m²

4.2.11 Klintgraven (X 791957, Y 7077378); 52,867 m²