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Identifying Conservative Criteria for (environmental) Assessments of Vulnerability;

Seabirds and Offshore Wind Farms as a Case
Study

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Identifying conservative criteria for (environmental) assessments of vulnerability; Seabirds and offshore wind farms as a case study

Master's thesis

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SUMMARY

There is an increasing interest in renewable energy from wind, in addition to a political pressure for increasing the renewable energy production within a short amount of time. Due to the fact that wind power plants are a new element in coastal areas, there is limited knowledge about the possible ecological consequences, particularly with regard to seabird populations. Accordingly there is a great need to provide adequate tools for assessing the vulnerability of areas in order to prioritize locations for establishment of wind plants. The main purpose of this study was to contribute to the development of a general framework to assess the vulnerability of wild species to human-induced installations and interference. The approach was based on a set of four vulnerability criteria: 1) Elasticity of adult and juvenile survival on the population growth rate, 2) Red list status, 3) Local abundances of seabird populations and 4) the variation of flight behavior among seabirds. I also investigated whether the different criteria differed based on geographic maps of the vulnerability in coastal areas in Norway, and the method presented in this study was compared to another framework for vulnerability assessment, developed by Garthe and Hüppop (2004). The present study contributes to a refined framework of vulnerability assessment, which to a larger extent consider the population dynamics of seabirds, compared to other methods based on multiple factor indexes. The study also contributes to the discussion of the methodological aspects of vulnerability assessments of seabirds.

INTRODUCTION

Wind power plants in coastal areas are a relatively new element in Europe, as well in Norway where the government in 2006 stated a common goal on an increase in renewable energy production at a total of 30 tWh within 2016 compared to 2001. An increase in energy produced by new wind power plants is an important part of this goal (Miljøverndepartementet 2007). However, at present there are few studies that have been performed on the short- and long-term effects of wind power plants on terrestrial and marine ecosystems and organisms. Thus, with an increasing interest in renewable energy from wind, there is also an increasing demand to investigate the possible ecological consequences of wind power installations on birds (e.g. Drewitt and Langston (2006)).

A substantial amount of the wind power plants have been established, or are planned to be established, in marine coastal areas as these provide optimal conditions for efficient utilization of wind power. Because these areas also may be important for many seabird species there is an urgent need to develop tools for detecting the most conflicting areas at an early stage of the planning process. In particular, it is important to develop, verify and revise adequate types of sensitivity indices to assess the vulnerability of animal species and nature types towards environmental alterations (Desholm 2009). These indices should, however, constantly be revised with regards to increasing knowledge of the impacts of wind power plants on seabird species.

Birds are assumed to be among the taxa most heavily affected by wind farms (Garthe and Hüppop 2004). Studies suggests that birds may be affected by wind farms both during migration, resting and foraging (Barrios and Rodríguez 2004) for instance by collisions or change or loss of habitat (Drewitt and Langston 2006). In seabirds, several factors may influence the vulnerability of a species such as seasonal variation in abundance, age distribution, behaviour and dispersal pattern, as well as life history traits such as reproduction and survival rates (Sæther and Bakke 2000, Garthe and Hüppop 2004, Fox et al. 2006, Desholm 2009). Seabirds, which in the presents study are defined in a wide sense (see methods), typically have life histories characterized by low productivity, delayed maturity, and relatively high adult survival probabilities (Weimerskirch 2002, Lee et al. 2008).

In general, the vulnerability of a population can be defined as its ability to maintain its natural population dynamics when exposed to an external influence, for instance caused by human activity (Kålås et al. 2010a). In long-lived species with delayed breeding, such as seabirds, population growth rate (λ) is most sensitive to survival rates, particularly adult

survival, and least sensitive to vital rates associated with reproduction (Lebreton and Clobert 1991, Pfister 1998).

Long-lived organisms are also characterized by relatively stable population size, and adult survival rates that varies relatively little between years (Gaillard et al. 2000, Sæther and Bakke 2000). Most seabirds fit this pattern, and population change tends to be slow (Weimerskirch 2002). Because of the typical life history characteristics of seabirds it makes them especially vulnerable from for instance environmental changes because even small decreases in adult survival will potentially have huge effects on the life time reproductive success of individuals (Wooller et al. 1992, Sandvik et al. 2008). In other words, an increased mortality among adults will have severe consequences for the population growth rates. Furthermore, when a large population reduction occur in populations of long-lived species, it takes several years until the population has stabilized at the carrying capacity of the habitat (provided sufficient food availability) (Begon et al. 2011).

Distribution of seabirds in Norwegian waters are determined by climatic, oceanographic, topographic and biological conditions. Due to the nutrient and fish rich waters outside the Norwegian coast about 2.9 million pairs of seabirds breeds along the coast with 48%, 44%, 5% and 3% in the Barents Sea, Norwegian Sea, North Sea and the Skagerrak, respectively (see Barrett et al. (2006), se also Systad et al. (2007), and Christensen - Dalsgaard et al. (2011) for a detailed account of seabird distribution and numbers along the Norwegian coast).

When assessing seabird vulnerability towards anthropogenic sources it is important to remember that potential threats are not only restricted to their breeding colonies. Some species (e.g. auks) forage within 100 km from the colonies, some (e.g. cormorants) forage within 30 km and others (e.g. common eiders) within the vicinity of their breeding sites (e.g. Cramp and Simmons (1983), Systad et al. (2007), Christensen - Dalsgaard et al. (2011)). Thus, when assessing the vulnerability of seabirds towards anthropogenic disturbances such as wind power plants their distribution on a large scale, e.g. during chick provisioning, should be addressed.

Four mechanisms have been recognized with regard to the impact of wind power plants on the population dynamics of bird populations (Drewitt and Langston 2006):

First, increased mortality resulting from collisions with wind turbines (tower and wings). Collision risk depends on factors related to bird species, numbers and behaviour, weather conditions and topography and the nature of the wind farm itself (Drewitt and Langston 2006). The risk is likely to be greater on or near areas regularly used by large numbers of feeding or roosting birds, or on migratory flyways or local flight paths. Birds with poor manoeuvrability

are generally at greater risk of collisions with structures (Bevanger 1994), and species that habitually fly at dusk or dawn or at night are less likely to detect and avoid turbines (Larsen and Clausen 2002). Risk also changes with weather conditions.

Second, displacement due to interference from installations in operation and from the activity associated with the construction and running of the wind power plants. Several studies have shown that the disturbance effect caused by wind farms varies greatly, and is likely to depend on a wide range of factors including seasonal and diurnal patterns among bird species, location with respect to important habitats, and availability of alternative habitats in addition to turbine/ wind farm specifications (Drewitt and Langston 2006 and references therein).

Third, loss and change of habitat through habitat degradation and fragmentation. The scale of direct habitat loss resulting from a constructing of a wind farm depends on the size of the project, but in general habitat loss per turbine case is likely to be small. Typical, actual habitat loss amounts to $2 - 5$ % of the total development area (Fox et al. 2006). In addition to direct habitat loss, several species will avoid an area with installations and structures, with the result of loss of access to important areas (Kaiser et al. 2006).

Fourth, barrier effects, may increase the flight distance and increase the birds' energy demands. This effect is of concern because of the possibility of increased energy expenditure when birds have to fly further, as a result of avoiding a large array of turbines, and the potential disruption of linkages between feeding, roosting, moulting and breeding areas otherwise unaffected by the wind farm (Fox et al. 2006).

Seabird vulnerability towards offshore wind power plants along the Norwegian coast was evaluated by Christensen - Dalsgaard et al. (2011) using a method called wind farm sensitivity index (WSI) originally developed by Garthe and Hüppop (2004) for German waters, which is a method based on multiple factor ranking (see description in appendix I). However, such methods containing multiple factor ranking schemes, often represents a methological problem due to multicolinearity among the factors that may obscure the interpretation of the index. For instance, 30.6% of the 36 different combination of the variables used in Garthe and Hüppop (2004) were intercorrelated (Desholm 2009). An other unfortunate property of the Garthe and Hüppop (2004) method is that as many as nine of the factors used are integrated into one index value, which can result in a loss of relevant information in the integration (Certain et al. 2012).

As an alternative to Garthe and Hüppop`s vulnerability index, Desholm (2009) presented an approach to evaluate seabird vulnerability towards wind power installations (with main focus on migrating species). This index is limited to two essential parameters: 1) a

measure of relative species specific abundance and 2) the species-specific sensitivity of population growth rate (λ) to changes in vital rates (fecundity and adult survival) based on a simplified stage-classified Leslie matrix model (Caswell 2001). Accordingly, this index will provide area-specific information on the parameters that determines the population`s ability to handle increased adult mortality. This approach appeals because it is based on a population projection matrix model (Caswell 2001), which provides a powerful tool to evaluate the consequences of how increaseed mortality rates due to turbine colission may potentially affect the population dynamics, measured as population growth rate (λ).

The red list status is another important assessment of the vulnerability of seabird species. Thus, species that are categorized as threatened on the national Red list (Kålås et al. 2010b), and potentially vulnerable to wind power plants must be managed with special care.

The aim of this thesis is to contribute to the development of a general framework to assess the vulnerability of wild species to man-made installations and human induced interference. I will base the approach on a set of four criteria, where the first three were selected because each of them have significant importance for the species` viability both locally and regionally: 1) the elasticity of adult and juvenile survival on the population growth rate, 2) the red list status, and 3) local abundances of seabird populations along the coast of Norway. In addition, I will also evaluate 4) the variation in flight properties among seabirds, which presumably has a substantial influence on the risk of colliding with wind turbines.

The approach based on the elasticity of the survival rates on the population growth rate is an established method that relate changes in vital rates in a population (survival rates, fecundity) directly to changes in population dynamics (measured as λ) (e.g. Caswell (2001). Given that some species have behavioural properties that make them more prone to collisions with wind farm turbines, I will be able to predict the magnitude of reduction in population growth rate (λ) given a certain reduction in survival rate. Accordingly, this method should presumably give a conservative and fundamental measure of the species specific consequences of increased mortality (due to for instance collisions with turbine blades) within an area.

First I will investigate the relationship between the elasticity of adult and juvenile survival and how they correlate with the species specific life history traits such as fecundity, survival rate of juveniles and adults, time to maturity, flight properties (manoeuvrability, flight altitude, night activity and time in air). Here I will both report observed correlations, but also linear regression analyses corrected for the phylogenetic relationships among species (Garland et al. 1992). These analyses reveal the strength of the elasticities in survival in relation to other life history traits. This is important in order to understand the underlying biological mechanism

of how increased mortality due to wind plants will potentially affect the vulnerability of the seabird species.

Secondly, based on the results from the previous analysis, I present maps showing the geographical distribution of seabird vulnerability based on survival elasticity, abundances, the red list status, as well as flight properties in order to evaluate their resemblance. Lastly I will present maps that demonstrate the contrasts between the WSI-method developed by Garthe and Hüppop (2004), and the four vulnerability criterias in the present study. Accordingly, this comparison of different vulnerability criteria will contribute to the discussion about which method is the most adequate for assessing vulnerability of seabird species towards the impact of wind plants along the Norwegian coast.

METHODS

Study species

The present study includes 20 characteristic seabird species that are commonly distributed along the Norwegian coast; 12 species from the order Charadriiformes, three species from the order Gaviiformes, two species from each of the order Anseriiformes and Suliformes and one species from the order Procellariiformes (Table 1.)

Study area and database

In this study, I used abundance data on seabird species that were collected along the whole coastline of Norway; including Skagerrak, The North Sea, the Norwegian Sea and the Barents Sea. The dataset was extracted from The Norwegian seabird registry, administrated by NINA. The dataset was organized in 10 x 10 km square grids, which contained monthly population proportions of the total Norwegian population of each of the species included in this study. These data were derived from the highest count of each species in each 10 x 10 km grid (for the 10-year period 2001-2010), divided by the national totals (G. H. Systad pers comm.). I used only abundance data from June as these were considered representative for the breeding season (S.-H. Lorentsen, G. H. Systad pers comm.).

Vulnerability indicators

Elasticity of survival on the population growth rate λ

The species-specific elasticity of a vital rate describes the effect of a change in a vital rate (i.e. survival probability or fecundity) on the proportional change in population growth rate (λ) (Caswell 2001, Desholm 2009). In the present study species-specific elasticity values for juvenile and adult survival were calculated according to a modified model presented by Desholm (2009), based on an age-structured Leslie matrix model (Caswell 2001), described in Appendix I. Assuming that $\lambda = 1$, which means that the population is in equilibrium over time makes it possible to calculate elasticity values also for species where data on specific vital rates are hard to obtain or lacking, as parameters (for instance fecundity, juvenile or adult survival rate, or time to maturity) can be set to give $\lambda = 1$, which has been shown not to influence the distribution of elasticities among species (Sæther and Bakke 2000). Such generalised and

relatively simple population Leslie matrix models have been shown to capture the essentials of full age-classified Leslie matrices (Brault and Caswell 1993, Levin et al. 1996, Heppell et al. 2000), and therefore represent a useful tool for a first assessment of the relative sensitivity to wind energy related mortality for different bird species.

Data for species-specific life history characteristics was obtained by surveying the literature (Table A, Appendix II). I aimed to obtain data from long term studies, preferably from Norwegian areas, or from areas as close to Norway as possible.

For individuals of a particular species who have reached age of maturity, the annual survival from one year to the next was defined as the adult survival (P_{ad}). Correspondingly, juvenile survival (P_{juv}) was defined as survival of the pre-productive life; from fledging to the time of breeding. However, juvenile survival rates were not required for estimating juvenile and adult elasticity, according to Eqn. 13 in Appendix I.

In this study the fecundity (F) was defined as the number of female offspring that fledged per adult female per season, assuming an equal sex ratio. This fecundity rate was not always reported in the literature, but typically as a ratio of "young fledging/ chicks per breeding pair", or as the "number of young fledged per year". Based on the assumption of an equal sex ratio, I adjusted such values to obtain a fecundity measure for females only. The age when females first started to breed was used as an estimate of age of maturity (N).

Red list status

The red list status of each species was scored according to Kålås et al. (2010b). I have classified the different red list categories with 0 = LC (least concern), 1 = NT (near threatened), 2 = VU (vulnerable), 3 = EN (endangered), 4 = CR (critically endangered). Thus, I assume that a high score on red list status correspond to a high vulnerability of the populations towards additional threats caused by wind power plants.

Flight properties

I used the vulnerability factors related to flight properties, and the scaling of the factors, reported by Garthe and Hüppop (2004), as they were considered especially important for seabird vulnerability towards wind power plants. These factors were evaluated on a scale ranging from 1 to 5, where 1 is low vulnerability and 5 is high vulnerability.

The manoeuvrability indicator considers the different species' ability to manoeuvre in air, especially in relation to avoid collisions with wind farms. High manoeuvrability is scored with a low value (1) and low manoeuvrability is scored with a high value (5) (see Garthe and Hüppop (2004). Accordingly, species with a high manoeuvrability score are assumed to have a higher risk of colliding with wind turbines.

The flight altitude indicator for the different species is based on classifications done under regular sea counts using binoculars. The variation in flight altitudes among species were classified according to Garthe and Hüppop (2004) where a higher score corresponded to a higher flight altitude and thus a higher vulnerability for collision with wind turbines.

Because the nightly flight activity indicator could not be quantified with real data it was subjectively classified on a scale from 1 to 5 according to Garthe and Hüppop (2004), with 1 representing almost no activity at all, and 5 representing high night activity. High nightly flight activity may presumably increase the vulnerability in relation to collisions with wind turbines.

The time spent in air indicator was also evaluated from counts along transects in open sea (Garthe and Hüppop 2004). The species specific classification was based on the proportion of birds that was observed flying in the transects (Garthe and Hüppop 2004).

Phylogenetic contrasts

When comparing the interrelationship in life history traits among species one have to account for the fact that species are phylogenetic related. The independent contrasts approach is designed to investigate the correlated evolution of traits that are inherited from ancestors (Garland et al. 1992). Because species are descended in a hierarchical fashion from common ancestors, they generally cannot be considered as independent data points in statistical analyses (Harvey and Pagel 1991, Garland et al. 1992). Thus, closely related species will tend to share more characters through common ancestry than through independent evolution (Harvey and Pagel 1991). The calculations for independent contrast method, developed by Felsenstein (1985) was conducted for all possible contrasts. Felsenstein (1985) proposed computing (weighted) differences ("contrasts") between the character values of pairs of sister species and/ or nodes, as indicated by a phylogenetic topology, and working down the (phylogenetic) tree from its tips (Garland et al. 1992). The calculations resulted in sixteen different contrasts, instead of 19, as expected (total number of species $n - 1$). The reason for this is that the relationship between species in the family Laridae (i. e. auks, gulls, terns, and skuas) under the order Charadriiformes is not clear. However, for this group, all possible contrasts within the

polytomy (i. e. branching) were calculated, and the mean value was used for conducting further contrasts. The standard deviation for the contrasts was calculated, which gives an indication of the branch length (Garland et al. 1992), and therefore an indication of the evolutionary change between the species.

Statistical analyses

All statistical tests were performed using SPSS (SPSS Inc. ver. 18.0). All tests were two-tailed and all values are reported as mean ($\pm$ SE).

First, I tested whether the distribution of elasticity for adult survival $e(P_{ad})$ and elasticity for juvenile survival $e(P_{juv})$ differed among the species included ($n = 20$) by performing a paired-sample t-test procedure. I then applied Pearson correlation analyses to analyse the observed relationship between the elasticity for both adult and juvenile survival ($E(P_{ad})$, $E(P_{juv})$, n = 20) and life history characteristics fecundity (F), juvenile survival (P_{juv}), adult survival (P_{ad}) and age of maturity (N). For all life history characteristics 20 species were included, except for P_{juv} where high quality data was available for only 10 species. Next I investigated the relationship between P_{ad} and P_{juv} elasticity by using Pearson correlations, and each of the flight properties categories (n = 20), which included manoeuvrability, altitude, time in air and night activity. Because of the similarities which appeared between maps of $e(P_{ad})$ and flight properties, I also examined whether there existed any correlations between the mean value of flight properties (calculated as (manoeuvrability* flight altitude*time in air* night activity)/4) and elasticity of P_{ad}. Next, I examined the relationship between the elasticity of P_{ad} and P_{juv} and red list status by Pearson correlation. Finally, I examined whether there existed any correlations among the different life history traits, as well as among the flight categories. However, because species cannot be considered as independent data points (Harvey and Pagel 1991), a linear regression analysis for the phylogenetic correction were carried out, testing the relationship between two variables of the contrasts (see Table C, Appendix II for dependent and explanative variables). Regressions of independent contrasts were forced through the origin (Garland et al. 1992). Accordingly, I analysed the correlations among the life history traits, flight properties and red list status, both based on the observed values in the dataset, and compared these correlations with the outcome from the dataset that were corrected for phylogenetic relatedness among the species.

The number of species included in the analyses varied; data on demographic traits included 20 species, except from juvenile survival, which was obtained for only 10 species. The dataset for phylogenetic data contained 16 different contrasts.

Calculations for creating maps

All maps were made using ArcGIS 10.1, by joining a grid by 10 x 10 km squares, with data sets which contained the square ID, in addition to all data needed to create the actual maps. The species specific abundance values were given as a proportion of the national abundance. The values were transformed to the natural logarithm (*ln(abundance + 1)*), in accordance with (Christensen-Dalsgaard et al. 2011). In order to interpret the geographical distribution of elasticity for adult survival ($e(P_{ad})$) the calculated elasticity values was multiplied with the species specific abundance (*ln(abundance + 1) * $e(P_{ad})$*). For flight properties the mean value of the four different flight properties, for each species was applied, and was then multiplied with the natural logarithm of abundance values (*(4 Flight properties / 4) * (ln (abundance value + 1))*).

In order to illustrate the total distribution of red list values of the selected species, I summarized all red list values (> Least concern) per 10 x 10 km square, excluding the abundance. Because increasing red list status is strongly related to declining populations (Kålås et al. 2010b), it was more interesting to investigate the geographic distribution of red list status, rather than including population sizes and abundance to the *red list* parameter.

In order to compare the geographical distribution of vulnerable areas depending on the different methods used, I applied the method developed by Garthe and Hüppop (2004) based on WSI. This method was implemented for the avifauna along the Norwegian coast by Christensen - Dalsgaard et al. (2011) by the use of a species-specific sensitivity index (SSI, see Appendix I). In order to calculate WSI, the SSI values were multiplied with the natural log of the population abundance for the breeding season (*SSI * ln (abundance breeding season + 1)*). In contrast to the method applied by Christensen - Dalsgaard et al. (2011), where regional species specific population fractions from the Barents Sea, the Norwegian Sea and the North Sea were applied, I have applied proportions of National population sizes.

Accordingly, I investigated whether the output of the WSI-method differed with the method based on elasticity developed through this study. In order to calculate the differences, I standardized all values using z-scores with a mean of 0 and a variance of 1, and then subtracted

the values of the different vulnerability indicators ($e(P_{ad})$, flight properties, abundance and red list status) from the WSI values. Finally, I obtained the values showing the differences, in maps, in order to show the geographical differences between the two methods applied.

Because of uncertainties in abundance data for some species (Northern fulmar, Arctic skua King eider, Red-throated diver, White-billed diver and Black-throated diver), these species are excluded from all maps. For maps of summarized red list status, all species > 0 (Least concern) are included (see table A, Appendix II). Therefore, for maps showing $e(P_{ad})$, flight properties flight properties and red list status, n = 14. However, the WSI values includes three more species (Great skua, Red-breasted Merganser and Northern Gannet).

RESULT

Distribution of life history characteristics of the selected species

There was substantial variation in the vital parameters of the study species reported from the literature (Table A, Appendix II). The data confirms the general result that juvenile survival rate is lower than the adult survival rate in seabirds. This pattern is further amplified because the juvenile stage refers to two or more years for several of the selected species. Correspondingly, the fecundity is generally low for the selected species.

The relationship between elasticities and life history characteristics assuming $\lambda = 1$

The distribution of elasticity for the juvenile and adult survival rates, respectively, differed significantly among the species (mean $e(P_{juv}) = 0.092$ (± 0.008), $n = 20$, mean $E(P_{ad}) = 0.674$, $SE = \pm 0.02$, $n = 20$), paired t-test; $t = 23,589$, $df = 19$, $P < 0.001$). This suggests that the average population growth rate (λ) was more sensitive to changes in adult mortality, compared to juvenile mortality for the selected species.

The relationship survival and the elasticity of juvenile survival was negative but not significant for the selected species ($r_p = -0.413$, $P = 0.070$, $n = 20$). Accounting for the phylogenetic relationships the corresponding regression analysis revealed a negative significant relationship between the phylogenetic contrasts of $e(P_{juv})$ on $e(P_{ad})$ ($\beta = -1.337$, $SE = \pm 0.334$, $df = 1$, $t = -3.881$, $P = 0.001$). This indicates that in species where the population growth rate was sensitive for changes in adult survival rate (i.e. high $e(P_{ad})$), the corresponding sensitivity for changes in juvenile survival rate was small.

Relative high elasticity in adult survival, $e(P_{ad})$, also occurred with species with high adult survival rate, $P_{ad,}$, and the correlation here was significantly positive ($r_p = 0.668$, $P = 0.001$, $n = 20$), which was also the case for the phylogenetic contrast regression analysis of P_{ad} on $e(P_{ad})$ ($\beta = 1.202$, $SE = \pm 0.222$, $df = 1$, $t = 5.410$, $P < 0.001$).

The elasticity in juvenile survival rates $e(P_{juv})$ were generally low ($e(P_{juv}) < 0.17$) (Table A, Appendix II). The highest elasticity in $e(P_{juv})$ occurred in species with low adult survival (P_{ad}) and low age of maturity (N). Accordingly, the relationship between $e(P_{juv})$ and P_{ad} was significantly negative ($r_p = -0.948$, $P < 0.0001$, $n = 20$), which was also the case for the relationship between $e(P_{juv})$ and age at maturity, N ($r_p = -0.722$, $P < 0.0001$, $n = 20$). These observed patterns for $e(P_{juv})$ were confirmed after accounting for phylogenetic relatedness; for

P_{ad} on $e(P_{juv})$ (β = -0.770, SE = ± 0.036, df = 1, t = -21.542 P < 0.001) and for N on $e(P_{juv})$ (β = -0.027, SE = ± 0.008, df = 1, t = -3.420, P = 0.004).

The relationship between elasticities and interspecific variation in flight properties.

Interestingly, a positive relationship was found between $e(P_{ad})$ and manoeuvrability (r_p = 0.522, P = 0.018, n = 20). Accordingly, this correlation indicates that for species with high elasticity in adult survival, generally had low manoeuvrability. However, this pattern was not confirmed after accounting for phylogenetic correction of manoeuvrability on $e(P_{ad})$ (β = 0.074, SE = ± 0.053, t = 1.395, P = 0.183), indicating that the significant pattern was due to the phylogenetic relationship among the species included in the study (Table C, Appendix II).

There were no significant correlations between $e(P_{ad})$ and altitude, night activity and time in air, respectively, as well as for the corresponding phylogenetic constrasts (Table B and C, Appendix II, respectively). Likewise, there were no significant relationships between $e(P_{juv})$ and any of the flight properties variables (all P > 0.05), also after correcting for phylogenetic relationships (P > 0.05 for all analyses, Table B and C, Appendix II respectively).

The relationship between elasticities and red list status

The results revealed no significant correlation was found between $e(P_{ad})$ and Red list status, as was also the case between $e(P_{juv})$ and Red list status (Table B, Appendix II). This indicates that for the species included, there was no relationship between the level of threat (measured as the red list status) and the sensitivity to changes in survival on the population growth rate.

Correlation among flight properties categories

A negative significant relationship was found between manoeuvrability and altitude among the species included (r_p = -0.531, P = 0.016, n = 20), indicating that a high vulnerability for manoeuvrability (i. e. poor manoeuvrability) was correlated with flight at low altitudes. Also, a negative significant relationship was found between manoeuvrability and night activity (r_p = -0.454, P = 0.044, n = 20). However, none of these relationships were significant when accounting for the phylogenetic relationships among the species, indicating that many of the species included were closely related. A complete overview over correlations and linear

regression coefficients of phylogenetic contrasts for elasticities, life history traits, flight properties and red list status are given in Table B and C in appendix II, respectively.

The geographical distribution of vulnerability indices

At the national level the distribution of vulnerability indices based on total abundance, the $e(P_{ad})$ and flight properties appeared to be quite accordant (Figure 1a, b, and c, respectively).

The maps showing distributions of total abundance, $e(P_{ad})$ and flight properties (Figure 1a, b and c) clearly identifies the areas around Gjesværstappen, Hjelmsøya and Lille Kamøy in Finnmark as the most significant areas when it comes to vulnerable areas for seabirds along the Norwegian coast during the breeding season. The species showing the highest vulnerability scores in these areas are auks, cormorants, fulmars and skuas. Further south, the areas around Nord-Fugløya, Vesterålen and Røst were highlighted with high vulnerability scores, mainly due to the large colonies of auks. In Helgeland, Sklinna and Vega turned out as important areas for auks and cormorants. In Froan, outside Trøndelag a large colony of black guillemots gave high vulnerability scores. In addition, this area was also important for cormorants and terns. Along the southwest coast of Norway, the areas around Runde, Nord-Øyane and Einevarden in Sogn og Fjordane had high vulnerability scores due to the large numbers of auks, cormorants, skuas and fulmars. In southern Norway, the areas with highest vulnerability scores were Jæren and Boknafjorden (mostly cormorants) and Lista and Rauna (gulls and terns).

The distribution of summarized red list status for species with status ≥ 1 (NT) clearly highlighted some regions where the total sum of red list status was high (13-14) (Figure 1d). These areas were from Sognefjorden to Runde and Nordøyane along the southwest coast of Norway, in Vega and Gåsvær and along the coast of northern Helgeland, in Vestfjorden between Lofoten and Salten, in most coastal areas outside Lofoten and Vesterålen up to Nord-Fugløya, and, finally in coastal areas around Lille Kamøy, Hjelmsøya, Gjesværstappan and Syltefjord in Finnmark (Figure 1d). In general, the distribution of red list status overlapped considerably with total abundance, eP_{ad}, and flight properties from Lofoten and further north.

Geographical distribution of total WSI (Figure 1e) revealed high values around Gjesværtappan, Hjelmsøya and Lille Kamøy in Finnmark, around Nord- og Sørfugløya in Troms, and in Vesterålen. Further south, areas with high WSI-scores were found in Røst, several smaller locations along the coast of Helgeland and in Froan outside Trøndelag. Also;

outside Runde, especially closest to the coast, and in Jæren and Lista high WSI-scores were found.

In order to compare the relative differences between WSI and the 4 vulnerability indices I subtracted the standardized values of the WSI and each of the 4 vulnerability indices. Thus, a high z-score indicates that the WSI-indices gives a higher vulnerability towards offshore wind power plants than the other vulnerability indices, and vice versa. The results demonstrated a generally high similarity between WSI and the total abundance, eP_{ad} and flight properties over large regions indicated by a difference between the values close to zero (Figure 2a, b and c). The geographic pattern of differences WSI and abundance, eP_{ad} and flight properties was quite similar, with z-scores close to zero. The regions around Runde, Vesterålen Hjelmsøya/ Gjesværstappan and Hornøya/ Reinøya were scored as more vulnerable (high z-scores) using the WSI approach. In contrast, larger areas along the coast of Nord-Troms and Finnmark (including Nordfugløy/Sørfugløy) were scored as more vulnerable using the approach based on abundances, $e(P_{ad})$ and flight properties (low z-scores). Similarly, in Helgeland (Sklinna and Vega) and Froan also scored as more vulnerable (low z-scores) by using the approach based on abundances, $e(P_{ad})$ and flight properties. However, the differences seemed to be stronger between WSI and flight properties, compared with $e(P_{ad})$ and abundances. Although the deviance between flight properties and WSI in a large degree shared the same geographical pattern, larger areas were considered more vulnerable according to WSI. Unlike for $e(P_{ad})$ and abundances, several areas along Helgeland, as well as the areas outside Sognefjorden, Jæren, Lista and the areas around Oslofjorden were considered vulnerable in with regard to flight properties (Figure 2c).

The largest difference in the distribution of vulnerability scores was found between the WSI approach and the red list status (Figure 2d). Areas outside Hornøya, Reinsøya, and Gjesværstappen, in addition to larger areas outside Lofoten and Vesterålen, and especially in Vestfjorden were scored as more vulnerable using the red list approach. Similar vulnerability scores were found for areas outside Rana, north of Runde to Sognefjorden, and finally, in a smaller area outside Jæren. Very few areas shared similar vulnerability patterns according to approaches relating red list status and WSI, meaning that quite large areas were considered vulnerable according to the WSI approach, with high z-scores (Figure 2d). These areas were located from east of Oslofjorden, and continued to an area south-west of Jæren, and further north in western parts of the coastline. With the exception of larger areas outside Rogaland (e.g. Jæren) and Sogn og Fjordane (e. g. Runde), the vulnerable areas were stretched from the shore to a large distance from land. Also, there were also vulnerable areas according to the WSI

approach outside Trøndelag, and further north, but then in a certain distance from land. Finally, similar areas were located outside Lille Kamøy and Hjelmsøya in Finnmark.

DISCUSSION

This study has documented high spatial variation in vulnerability of seabird species towards potential establishment of wind power plants along the coast of Norway. Such knowledge is crucial in order to make recommendations to management authorities about where the consequences of wind parks on the local avifauna will have minimal ecological consequences. The four vulnerability indices I considered was 1) the elasticity of adult and juvenile survival on the population growth rate, 2) the red list status, and 3) local abundances of seabird populations along the coast of Norway. In particular I emphasized the elasticity of survival on the local population growth rate ($e(P_{ad})$ and $e(P_{juv})$). The advantage of using this approach is that it directly links the effect of increased mortality due to collisions with the predicted effect on the species specific population growth rate (λ), based on an age-structured Leslie matrix model (Caswell 2001). Accordingly, this is a much more fundamental approach compared to using more proximate vulnerability indices that typically relates different species specific properties to the risk of collision. Interestingly, the study demonstrate a large extent of overlap between the four vulnerability indices, whereas the distribution of red list status among areas deviate most from the other vulnerability indices involved. I also recommend a balanced approach that combine the use of complex vulnerability indices (such as WSI) with important but more specific indices such as the elasticity of survival and the red list status as a tool for assessing the vulnerability of species.

The results revealed that elasticity for juvenile and adult survival was significantly negative correlated (Table B, Appendix II and Table C, Appendix II). This was as predicted, because in long-lived organisms, a given proportional change in juvenile survival is known to have much less effect on population growth rate than the same proportional change in adult survival (Gaillard et al. 2000, Sæther and Bakke 2000, Eberhart 2002). Furthermore, in many species with long generation time, life histories are characterized by low elasticity for juvenile survival and high elasticity for adult survival (Gaillard et al. 2000), which implies that population growth rates are less sensitive to change in juvenile survival than to the same change in adult survival (Lebreton and Clobert 1991).

Among the study species the analyses revealed that the elasticity for adult survival was positively related to adult survival rate and negatively related to elasticity in juveniles (Table B, Appendix II and Table C, Appendix II). These relationships were also expected and have been documented in previous studies (Heppell et al. 2000 and Sæther and Bakke 2000). Additionally the elasticity in juvenile survival decreases as age of maturity increases. According

to Heppell et al. (2000), juvenile survival elasticities, as well as fertility elasticities, are strongly correlated with age of maturation and life expectancy (Heppell et al. 2000).

Interestingly, the present study revealed no significant relationships between elasticity for adult survival and red list status, as well as flight categories, except from a significant positive correlation between elasticity for adult survival and manoeuvrability (Table B, Appendix II) However, the lack of a significant relationship after accounting for the phylogeny indicated that the positive correlation was due to relatedness among the species included in the study (Table C, Appendix II).

Many studies that assess vulnerability in conservation management have attempted to integrate multiple factors into a simplified vulnerability index (Lambeck 1997, Cowling et al. 2003). This may lead to unjustifiable weighing of factors against each other (Faith and Walker 1996). Multiple ranking schemes also may suffer from unintentional weighing because of multicolinerarity among variables (Beissinger et al. 2000), which is observed in the study of Garthe and Hüppop (2004). This is an example of combining scores for multiple factors with different and incompatible currencies, where there is no justifiable way of weighing them against each other (Faith and Walker 1996). These problems could be avoided by integrating the relating factors within as few common currencies as possible (Williams and Araújo 2002).

The distribution of abundance (Figure 1a) identified important areas with high total abundances of seabirds in the breeding season along the Norwegian coast. However, when the summed log abundances were included as a component of the vulnerability index, the log abundance seemed to dominate the results (Figure 1b, c and e).This problem has also been discussed by Certain et al. (2012) who suggested that the WSI index may imply a loss of important information by the way the factors and abundances are integrated. The consequence may be that the decision making in conservation management would be largely based on summed log-abundance, instead of accounting for the documentation for all the risk factors through SSI (Certain et al. 2012). This phenomenon can be observed in the present study, for instance, through the distribution of red list status, which clearly differentiated from the distribution of total WSI (Figure 1d). Red list status is one factors included in the WSI index, and this indicates that WSI did not fully account for several important geographical areas in relation to summed red list status for seabirds occurring in the area. In the WSI index, species specific information and abundances are being mixed together, and Certain et al. (2012) therefore suggests leaving abundances aside, and instead apply geographical distributions of abundances as a natural supplement together with each vulnerability factor.

The vulnerability indices based on distribution of elasticity for adult survival and flight properties were almost identical, indicating that in areas with high elasticity for adult survival, there was also a high vulnerability based on flight properties, as was indicated by a significant positive correlation (Table B, Appendix II). In areas with high vulnerability according to flight properties one can assume a higher risk of seabird collisions with wind farm installations, which is an important aspect for vulnerability assessments. However, because of the similarities with the distributions of elasticity for adult survival, flight properties will not provide further information in relation to vulnerability for wind farms, and therefore, elasticity for adult survival will probably give sufficient information in that regards.

The average vulnerability scores based on flight behavior revealed small differences between the species (Table A, appendix II). However, these differences appeared larger when separating the different flight categories used. In general, auks appeared least vulnerable judged on their flight behavior, while herring gull and black-throated diver appeared most vulnerable. Different environmental climatic impacts can affect the energetic costs of flying in regards to different styles of flying. For instance strong wind can be beneficial for gliding species (Furness and Bryant 1996) but can have opposite effect on flapping species (Gabrielsen et al. 1987).

The reproduction period is energetically stressfull for seabirds, with an increased energy demand (Durant et al. 2004). Often, there are long distances between the breeding colonies and the foraging areas, and during periods with low food availability, flight properties becomes increasingly important because only species with low flight costs may be able to move between patches and over longer distances (Durant et al. 2004).

For most seabird species, little knowledge exists in regards to mortality due to collision risk among seabird species, and the effects of an offshore wind farm due to disturbance, barrier effects and habitat loss (Drewitt and Langston 2006). However, some studies have suggested that several bird species are most likely to avoid the wind farm installation. Accordingly, one might suggest that offshore wind farm installations will be disturbing for several sea bird species, leading to increased energetic costs because of longer alternative flight patterns in an attempt to avoid the wind farm, which again can have negative effects on the chicks due to less food supply. In addition, wind and weather conditions can affect flight patterns, which can result in increased mortality. However, more research is required on how offshore wind farms might affect seabirds (Christensen - Dalsgaard et al. 2011).

In the present study I found that large areas along the coast indicated high total red list status among the species present (Figure 1d), meaning that ≤ 7 different species with a red list status ≥ LC (Least concern) were present in the areas with highest values. Quantitative analysis

of extinction risk is one of the criteria for risk categorization used by IUCN (International Union for the Conservation of Nature). Most species are classified by population size, in addition to observed population decline or habitat loss (IUCN 1996). For instance, Common guillemot (CR), Black-legged kittiwake (EN), Razorbill (VU) and Atlantic Puffin (VU) were qualified with red list status based on population declines (Artsdatabanken 2010). Even though the red list status is important as a vulnerability measure in itself, it did not correlate with the other parameters related to vulnerability related to wind plants (Table B, Appendix II). However, the red list classification does not provide sufficient guidance for optimizing management efforts (Mace and Hudson 1999) in relation to demographic information (Heppel et al. 2000).

In the present study the maps are presented on a large scale, which is useful for highlighting vulnerable areas on a national scale. However, locally important areas might be less visible on this scale (Christensen - Dalsgaard et al. 2011). Therefore, large-scale vulnerability assessments must always be used only as an indication, and assessments of vulnerability in local areas must be assessed based on local surveys of the avifauna.

Although a multifactor vulnerability index such as WSI (Garthe and Hüppop 2004) is very useful in identifying vulnerable areas, the method has been criticized. For instance, by using a WSI index, rare species will first be up weighted in the SSI index through their status, but then again down weighted through the use of abundances through WSI since they are less abundant. In contrast, abundant species will be down weighted through SSI, but then up weighted through WSI (Certain et al. 2012). Also, the use of log abundance assumes that the importance of a single seabird in a location decreases exponentially as the total number of seabird in that location increases. A solitary individual in an area will have more weight than an individual located in a large group of birds (Certain et al. 2012).

The log abundance has also been multiplied into the flight property index (Figure 1c) and the elasticity of adult survival index (Figure 1b) in the present study (but not the red list status index, Figure 1d). However, the simplicity of these indices compared with the WSI makes them attractive. In particular the elasticity of the adult and juvenile survival ($e(P_{ad})$ and $e(P_{juv})$)is an important contribution because it is founded on species specific vital life history parameters and indicate the projected consequences on species specific population growth rate. Accordingly, I recommend that one should pay particular attention to the elasticity index, and how it may compliment to other vulnerability indices, for instance WSI (Figure 2b).

In regard to management authorities, there is a demand for simplified and synthesized vulnerability assessments (Piatt et al. 2007). However, the disadvantage is that one attempts to synthesize several vulnerability indicators into one single vulnerability index (Certain et al. 2012). The present study suggests that important information related to spatial distribution of seabirds can be synthesized in a few sets of maps which emphasize the contrasting patterns between vulnerability indices such as the contrast between WSI and elasticity of adult survival (Figure 2b) and the contrast between WSI and the red list status (Figure 2d) (Certain et al. 2012). Such an approach may help managers to make a more balanced assessment of the vulnerability which both accounts for the complexity of multiple factors (for instance WSI) but also accounts for important information related to specific indices such as the distribution of red list status and the elasticity of adult survival probability on the population growth rate.

In addition, the approach presented in this study may be implemented to provide a general framework for vulnerability assessment, which may be applied to comparable situations beyond offshore wind energy assessment, for other types of impacts, and other taxa, where ecological consequences of physical interventions in the wild are assessed in general.

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Table 1

List of seabird species from the Norwegian coast, in systematic order.

Nr.	Name	Latin name	Family	Norwegian name
Charadriiformes Ord. (vaders, gulls, auks)				
1.	Black-legged kittiwake	*Rissa tridactyla*	Lariidae (gulls)	Krykkje
2.	Herring gull	*Larus argentatus*	Lariidae	Gråmåke
3.	Great black-backed gull	*Larus marinus*	Lariidae	Svartbak
4.	Lesser black-backed gull	*Larus fuscus*	Lariidae	Sildemåke
5.	Common gull	*Larus canus*	Lariidae	Fiskemåke
6.	Razorbill	*Alca torda*	Alcidae (auks)	Alke
7.	Atlantic puffin	*Fratercula arctica*	Alcidae	Lunde
8.	Black guillemot	*Cepphus grille*	Alcidae	Teist
9.	Common guillemot	*Uria aalge*	Alcidae	Lomvi
10.	Common tern	*Sterna hirundo*	Sternidae (terns)	Makrellterne
11.	Arctic tern	*Sterna paradisaea*	Sternidae	Rødnebbterne
12.	Arctic skua	*Stercorarius parasiticus*	Stercorariidae	Tyvjo
13.	Great skua	*Sternocorarius skua*	Sternicoriidae	Storjo
Gaviiformes Ord. (Divers)				
14.	White-billed diver	*Gavia adamsii*	Gavidae	Gulnebblom
15.	Red-throated diver	*Gavia stellata*	Gavidae	Smålom
16	Black-throated diver	*Gavia arctica*	Gavidae	Storlom
Anseriiformes Ord. (Ducks)				
17.	Common eider	*Somateria mollissima*	Anatidae	Ærfugl
18.	King eider	*Somateria spectabilis*	Anatidae	Praktærfugl
19.	Red-breasted merganser	*Mergus serrator*	Anatidae	Siland
Pelicaniformes Ord. (Pelicans, cormorants)				
20.	European shag	*Phalacrocorax aristotelis*	Phalacroracidae	Toppskarv
21.	Great cormorant	*Phalacrocorax carbo*	Phalacroracidae	Storskarv
Procellariiformes Ord. (Storm birds)				
22.	Northern fulmar	*Fulmarus glacialis*	Procellariidae	Havhest
Pelecaniformes Ord.				
23.	Northern gannet	*Morus basssanus*	Sulidae	Havsule

Figure 1: Maps showing the distribution of vulnerability of seabird species along the Norwegian coast (n = 14, except for WSI; n = 17), according to a) abundance, b) elasticity of adult survival, c) flight properties, d) red list status, and e) total WSI. All values are standardized using z-scores with a mean of 0 and a variance of 1. Very high/ low scores are caused by extreme values.

Figure 2: Maps showing differences in vulnerability of seabird species along the Norwegian coast (n = 14, except for WSI; n = 17), between a) abundance and WSI, b) elasticity of adult survival and WSI, c) flight properties and WSI and d) red list status and WSI. The relative differences are calculated by subtracting the standardized values of the WSI and each of the 4 vulnerability indices. High z-scores indicates that WSI-indices gives a higher vulnerability towards offshore wind power plants than the other vulnerability indices (red areas), and vice versa (blue areas).

Figure 1
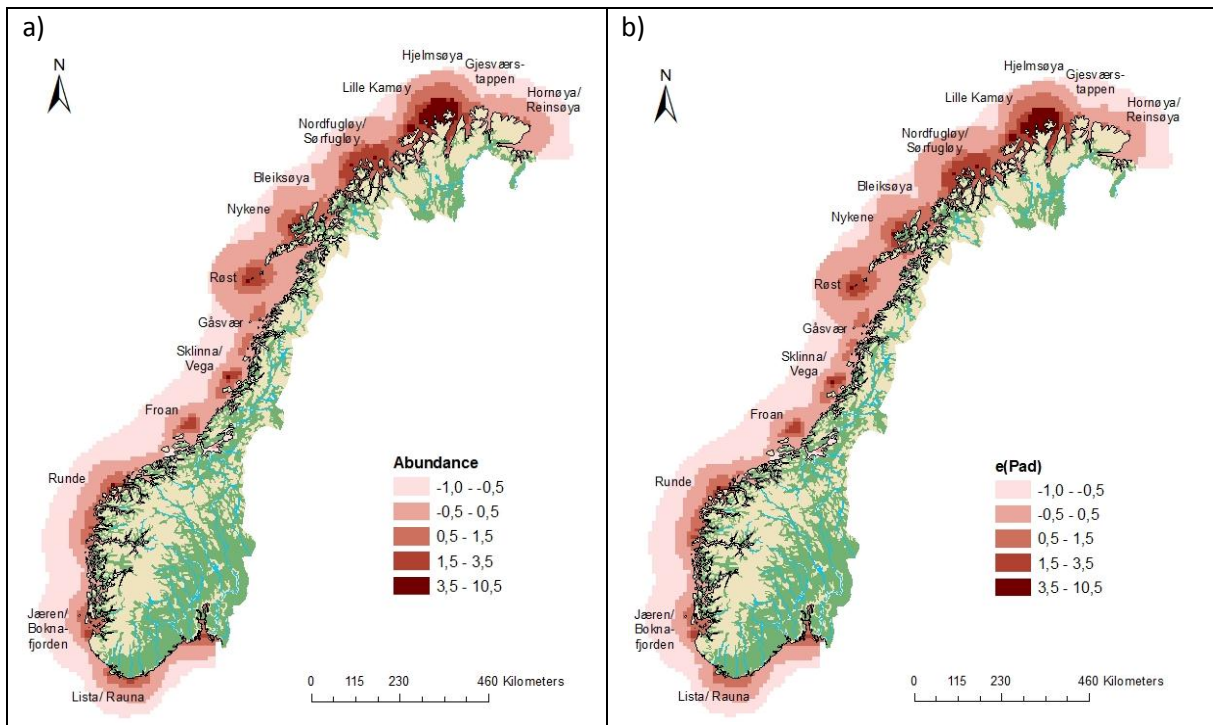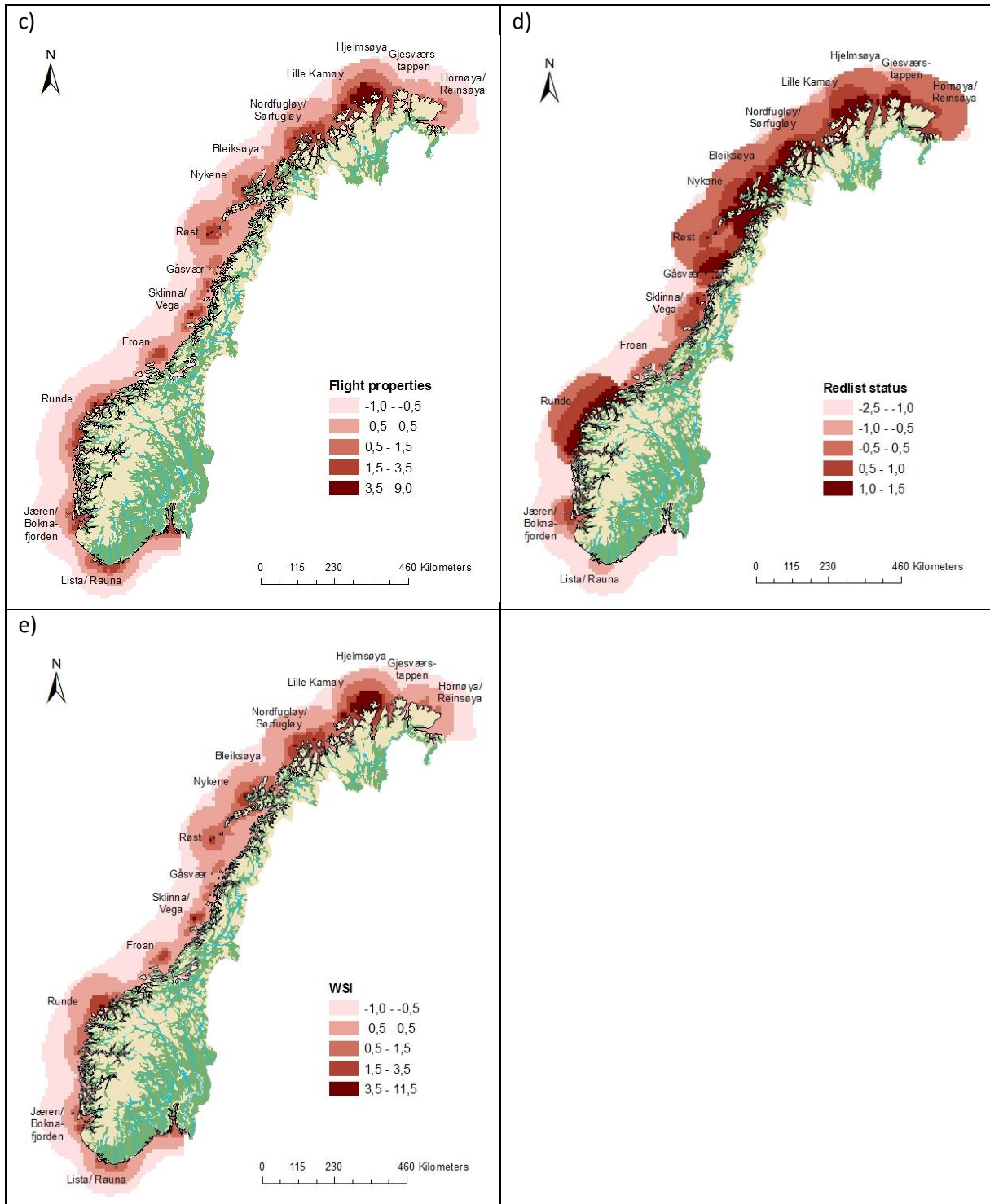
Figure 2
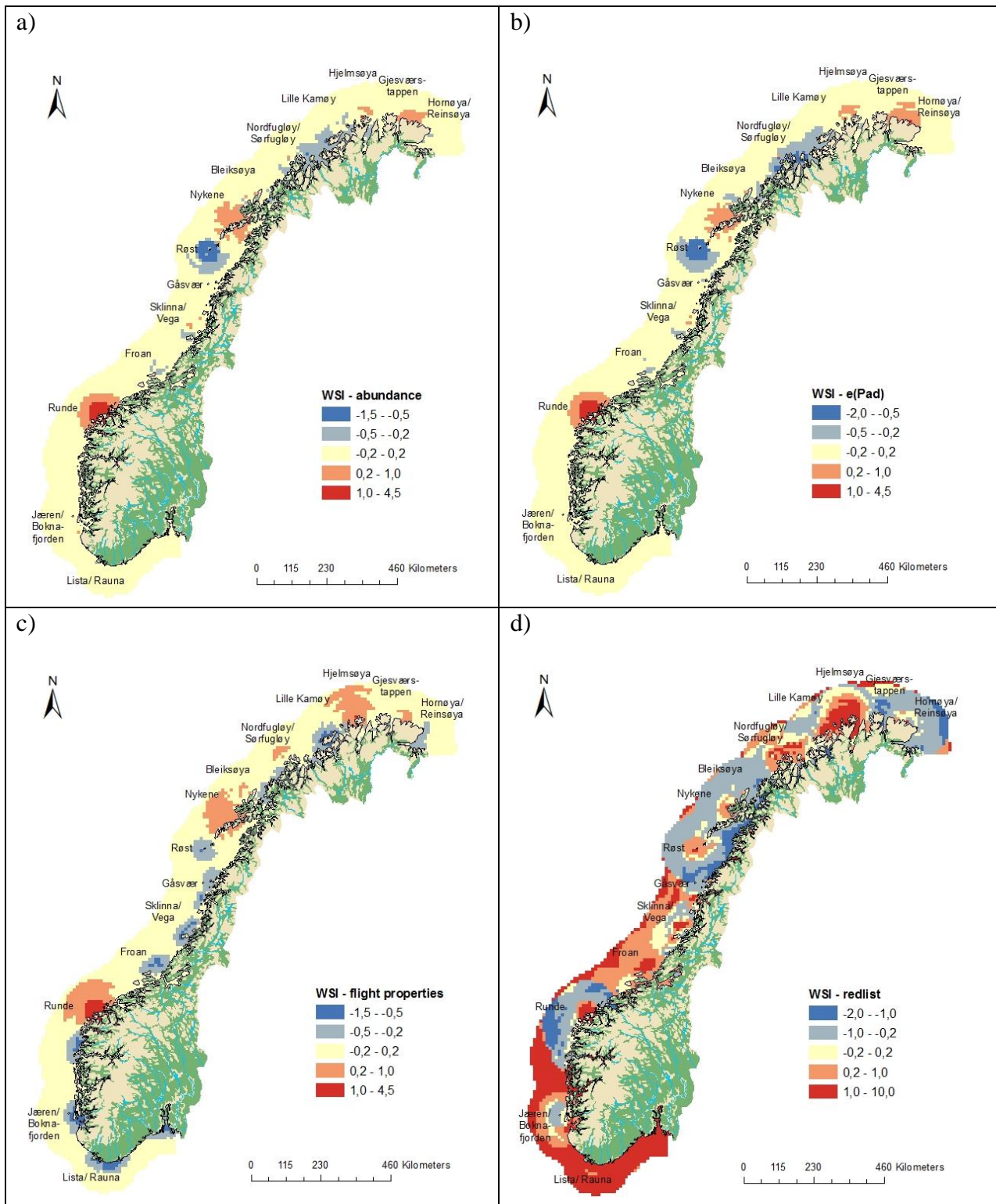
The Garte and Hüppop (2004) method

It provides a species-specific vulnerability index (SSI) based on nine factors: flight maneuverability (*a*), flight altitude (*b*), percentage of time flying (*c*), nocturnal flight activity (*d*), sensitivity towards disturbance by ship/helicopter traffic (*e*), flexibility in habitat use (*f*), bio-geographical population size (*g*), and adult survival rate (*h*) and conservation status (*i*), respectively. The SSI was calculated as:

$$SSI = \frac{(a+b+c+d)}{4} \times \frac{(e+f)}{2} \times \frac{(g+h+i)}{3}$$

The SSI's for all species resident in an area were then combined with a measure of population density (given as the relative proportion of the specific seabird species in an area) to obtain a (site specific) wind power plant sensitivity index (WSI):

$$WSI = \sum_{species} (\ln (density_{species} + 1) \times SSI_{species})$$

Calculations for finding species specific elasticity for adult and juvenile survival

(By Jarle Tufto, Professor of Statistics, NTNU)

We consider an age-structured model with n age-classes and Leslie matrix

$$L = \begin{bmatrix} & & & FP_0 \\ P_1 & & & \\ & \ddots & & \\ & & P_{n-1} & P_{ad} \end{bmatrix}.$$

(1)

The number of in age –class n (adults) are at time $t + n$ can then be written as

$$N_{n,t+n} = P_{ad}N_{n,t+n-1} + F \prod_{i=0}^{n-1} P_i N_{n,t}$$

(2)

The corresponding characteristic equation obtained by setting $N_{n,t} = c\lambda^t$ becomes

$$\lambda^n = P_{ad}\lambda^{n-n} + F P_{juv},$$

(3)

where $P_{juv} = \prod_{i=0}^{n-1} P_I$.

If we require that the growth rate of the population $\lambda = 1$, it follows that any of the three parameters F, P_{ad} and P_{juv} if missing, can be expressed as

$$F = \frac{1-P_{ad}}{P_{juv}}, \quad P_{juv} = \frac{1-P_{ad}}{F}, \quad P_{ad} = 1 - FP_{juv},$$

(4)

given estimates of the two remaining parameters.

The sensitivities of λ to changes in F, P_{ad} and P_{juv} can be found be implicit differentiation. Differentiating (3) with respect to F gives

$$N\lambda^{n-1}\frac{\partial\lambda}{\partial F} = P_{ad}(n-n)\,\lambda^{n-2}\frac{\partial\lambda}{\partial F} + P_{juv},$$

(5)

which solved for $\frac{\partial\lambda}{\partial F}$ yields the sensitivity

$$\frac{\partial\lambda}{\partial F} = \frac{P_{juv}}{n\lambda^{n-1} - P_{ad}(n-1)\lambda^{n-2}} \xrightarrow{\lambda=1} \frac{P_{juv}}{n - P_{ad}(n-1)},$$

(6)

and the elasticity

$$\frac{\partial \ln \lambda}{\partial \ln F} = \frac{\partial \ln \lambda / \lambda}{\partial \ln F / F} = \frac{F P_{juv}}{n\lambda^n - P_{ad}(n-1)\lambda^{n-1}} \xrightarrow{\lambda=1} . \tag{7}$$

From (3) we obtain similar expressions for the sensitivity and elasticity to changes in P_{juv},

$$\frac{\partial \lambda}{\partial P_{juv}} = \frac{F}{n\lambda^{n-1} - P_{ad}(n-1)\lambda^{n-2}} \xrightarrow{\lambda=1} \frac{F}{n - P_{ad}(n-1)}, \tag{8}$$

and

$$\frac{\partial \ln \lambda}{\partial \ln P_{juv}} = \frac{F P_{juv}}{n\lambda^n - P_{ad}(n-1)\lambda^{n-1}} \xrightarrow{\lambda=1} \frac{F P_{juv}}{n - P_{ad}(n-1)}. \tag{9}$$

Differentiating (3) with respect to P_{ad} leads to

$$n\lambda^{n-1}\frac{\partial \lambda}{\partial P_{ad}} = \lambda^{n-1} + P_{ad}(n-1)\lambda^{n-2}\frac{\partial \lambda}{\partial P_{ad}}, \tag{10}$$

or

$$n\lambda\frac{\partial \lambda}{\partial P_{ad}} = \lambda + P_{ad}(n-1)\frac{\partial \lambda}{\partial P_{ad}}. \tag{11}$$

Solving the sensitivity yields

$$\frac{\partial \lambda}{\partial P_{ad}} = \frac{\lambda}{n\lambda - P_{ad}(n-1)} \xrightarrow{\lambda=1} \frac{1}{n-(n-1)P_{ad}}, \tag{12}$$

and the elasticity

$$\frac{\partial \ln \lambda}{\partial \ln P_{ad}} = \frac{P_{ad}}{n\lambda - P_{ad}(n-1)} \xrightarrow{\lambda=1} \frac{P_{ad}}{n - P_{ad}(n-1)}. \tag{13}$$

Finally we consider the sensitivity and elasticity of λ to simultaneous changes in all juvenile and adult survival rates $P_0,.., P_{n-1}$ and P_{ad}. Since the discrete time model must be regarded as

an approximation of a continuous time process, it is worth first considering how a change in the instantaneous hazard rate in a continuous time model jointly would influence the different survival rates. If the hazard rate is $h(t)$ at age t, then the ith survival rate

$$P_i = e^{-\int_i^{i+1} h(t)dt} \tag{14}$$

If the effect of wind farms is to increase the hazard rate additively by an amount of Δh, then this changes all P_i to

$$e^{-\int_i^{i+1} h(t) + \Delta h)dt} \tag{15}$$

that is, multiplicatively by a factor of $e^{-\Delta h}$. An additive effect on the hazard $h(t)$ is a somewhat unconventional assumption; more standard methods of survival analysis often assume that different effects acts multiplicatively on the hazard, for example, Cox's proportional hazards model. In terms of windmill collations, however, an additive effect on the hazard may be reasonable since these forms of accidents are thought to occur almost independently of other sources of mortality.

A small multiplicative change on all P_is and P_{ad} can be modelled by replacing these parameters by αP_i and αP_{ad} in in the original model. Keeping in mind that P_{juv} is a product of n survival rates, this changes the characteristic equation (3) to

$$\lambda^n = \alpha P_{ad} \lambda^{n-1} + F \alpha^n P_{juv}. \tag{16}$$

Implicit differentiation with respect to α now yields

$$N\lambda^{n-1}\frac{\partial\lambda}{\partial\alpha} = P_{ad}\lambda^{n-1} + \alpha P_{ad}(n-1)\lambda^{n-2}\frac{\partial\lambda}{\partial\alpha} + FP_{juv}n\alpha^{n-1}, \tag{17}$$

And sensitivity and elasticity

$$\frac{\partial \ln\lambda}{\partial \ln\alpha} = \frac{\partial\lambda}{\partial\alpha} = \frac{P_{ad} + FP_{juv}\,n}{n - P_{ad}\,(n-1)} \tag{18}$$

for $\alpha = 1$ and $\lambda = 1$.

Table A: List over species, and values for life history characteristics (juvenile and adult survival (P_{juv}, P_{ad}), fecundity (F) and age to maturity (N), as reported in literature (see reference below). Next, elasticities for adult survival and juvenile survival ($e(P_{ad})$ and $e(P_{juv})$). Continuing, flight categories (*Manouver*, *Altitude*, *Night activity* and *Time in air*) scored according to estimations in NINA report 616 (Christensen-Dalsgaard et al. 2011), with increasing value for vulnerability. Also, mean scores for flight properties are estimated. Finally, red list status, scored according to the National red list (Kålås et al. 2010), with 0 = Least concern, 1 = Near threatened, 2 = Vulnerable, 3 = Endangered and 4 = Critical.

								Flight properties*					
Nr	Name	F	P_{juv}	P_{ad}	N	$E(P_{ad})$	$E(P_{juv})$	Manouver	Altitude	Night activity	Time in air	Mean flight prop.	Red list **
1	Common eider [a]	0,2		0,80	2	0,6667	0,1667	4	1	2	3	2,5	0
2	King eider [b]	0,24	0,67	0,94	3	0,8393	0,0536	4	1	2	3	2,5	0
3	Red-throated diver [c]	0,23		0,84	2	0,7241	0,1379	5	2	2	1	2,5	0
4	Black-throated diver [d]	0,1		0,85	2	0,7391	0,1304	5	2	3	1	2,75	1
5	White-billed diver [e]	0,56		0,9	4	0,6923	0,0769	5	2	2	1	2,5	1
6	Northern fulmar [f]	0,18	0,88	0,94	8	0,6620	0,0423	3	1	2	4	2,5	1
7	Great cormorant [g]	1,22		0,852	4	0,5900	0,1025	4	1	4	1	2,5	0
8	European shag [h]	0,55	0,44	0,87	2	0,7699	0,1150	4	1	3	1	2,25	0
9	Arctic skua [i]	0,61	0,72	0,8	4	0,5000	0,1250	1	3	5	1	2,5	1
10	Atlantic puffin [j]	0,35	0,933	0,943	5	0,7679	0,0464	3	1	1	1	1,5	2
11	Black guillemot [k]	0,6	0,79	0,87	4	0,6259	0,0935	4	1	1	2	2	2
12	Razorbill [l]	0,38	0,814	0,919	4	0,7393	0,0652	4	1	1	1	1,75	2
13	Common Guillemot [m]	0,39	0,82	0,926	6	0,6759	0,0540	4	1	1	2	2	4
14	Common tern [n]	0,65	0,35	0,91	4	0,7165	0,0709	1	2	5	1	2,25	2
15	Arctic tern [o]	0,19		0,87	4	0,6259	0,0935	1	1	5	1	2	0
16	Black-legged kittiwake [p]	0,6	0,79	0,85	5	0,5313	0,0938	1	2	3	3	2,25	3
17	Common gull [q]	0,1		0,8	3	0,5714	0,1429	1	3	2	3	2,25	1
18	Lesser black-backed gull [r]	0,12		0,838	4	0,5639	0,1090	1	4	2	3	2,5	0
19	Herring gull [s]	0,3		0,93	5	0,7266	0,0547	2	4	2	3	2,75	0
20	Great black-backed gull [t]	0,48		0,93	4	0,7686	0,0579	2	3	2	3	2,5	0

* Christensen – Dalsgaard et al. (2011)
** Kålås et el. (2010b)
[a] Cramp (1977)

[b] *P*: Oppel et al. 2010. *N*: Cramp (1977) *F*: Grand and Flint (1997)

[c] del Hoyo (1992). P_{ad}: Hemmingsson et al. (2002)

[d] del Hoyo (1992), Nilsson (1977), Hemmingsson et al. (2002)

[e] P_{juv}, P_{ad}: Lavers et al. (2009). *F*: North et al. (1988). *N*: North (1994)

[f] Dunnet et al. (1979), Dunnet and Ollason (1978)

[g] *F*: Budworth et al. (2000). P_{ad}: Fredriksen and Bregnballe (2000). *N*: Cramp (1977)

[h] Aebischer (1986), Harris et al. (1994a)

[i] O'Donald (1983)

[j] *F*: Barrett et al. (2009), (2010). P_{juv}, P_{ad}: Sandvik et al. (2008). *N*: Harris (1984)

[k] P_{juv}, *N*: Cramp (1985). P_{ad}: Frederiksen et al. (1999). *F*: Ewins (1988)

[l] *N*: Cramp (1985) *F*: Barrett et al. (2009, 2010). P_{juv}: Lyngs (1994). P_{ad}: Sandvik (2005)

[m] *N, F*: Harris and Wanless (1988), (1995), Harris et al. (1994b). P_{juv}: Crespin et al. (2006), P_{ad}: Sandvik et al. (2005)

[n] *F, P_{ad}, P_{juv}*: Becker et al. (2001). *N*: del Hoyo (1996)

[o] Coulson and Horobin (1976)

[p] Coulson and White (1959), Coulson and Wooller (1976), Wooller and Coulson (1977), Thomas (1983).

[q] Cramp (1983), Del Hoyo (1996)

[r] *F, P_{ad}*: Perrins and Smith (2000). *N*: Cramp (1983)

[s] *F*: Cramp (1983). *N*: Del Hoyo (1996). P_{ad}: Gutz von Blotzheim et al. (1982)

[t] P_{ad}: Gutz von Blotzheim and Bauer (1982). *F*: Barrett et al. (2009), (2010). *N*: Cramp (1983)

Table B: Pearson correlation coefficients (r_p) between life history characteristics, flight properties factors and red list status of seabird species (n = 20, except for P_{juv}; n = 10).

	P_{juv} (n= 10)	P_{ad}	N	$e(P_{ad})$	$e(P_{juv})$	Manoeuvrability	Altitude	Night activity	Time in air	Red list status
F	- 0.518	0.012	0.087	- 0.212	- 0.115	- 0.056	- 0.200	0.341	- 0.380	0.137
P_{juv}		0.212	0.620	0.220	- 0.412	0.231	- 0.256	- 0.675*	0.368	0.365
P_{ad}			0.546*	0.668**	- 0.948**	0.166	- 0.232	- 0.349	0.094	0.227
N				- 0.202	- 0.722**	- 0.281	- 0.040	- 0.150	0.374	0.460*
$e(P_{ad})$					- 0.414	0.522*	- 0.290	- 0.358	- 0.110	- 0.167
$e(P_{juv})$						0.047	0.132	0.260	- 0.150	- 0.328
Manoeu-vrability							- 0.531*	- 0.454*	- 0.295	- 0.029
Altitude								0.096	0.282	- 0.260
Night activity									- 0.361	- 0.239
Time in air										- 0.086

Asterisks indicate significant correlations: * P < 0.05, ** P < 0.01.

Table C: Linear regressions of independent contrasts, between life history characteristics, flight behavior factors and red list status of seabird species (n = 16).

Dependent Variable	Explanative variable	β	SE (standard error)	t	P	R^2
$e(P_{ad})$	P_{ad}	1.202	0.222	5.410	<0.001	0.661
$e(P_{ad})$	F	0.013	0.104	0.129	0.900	0.001
$e(P_{ad})$	N	0.004	0.020	0.217	0.831	0.003
$e(P_{juv})$	P_{ad}	-0.770	0.036	-21.542	<0.001	0.969
$e(P_{juv})$	N	-0.027	0.008	-3.420	0.004	0.438
$e(P_{ad})$	Manoeuvrability	0.074	0.053	1.395	0.183	0.115
$e(P_{ad})$	Altitude	0.032	0.055	0.579	0.571	0.022
$e(P_{ad})$	Night activity	-0.023	0.060	-0.378	0.711	0.009
$e(P_{ad})$	Time in air	-0.044	0.049	-0.895	0.385	0.059
$e(P_{juv})$	Manoeuvrability	-0.012	0.029	-0.420	0.680	0.012
$e(P_{juv})$	Altitude	-0.007	0.029	-0.237	0.816	0.004
$e(P_{juv})$	Night activity	0.018	0.032	0.568	0.578	0.021
$e(P_{juv})$	Time in air	-0.011	0.027	-0.401	0.694	0.011
P_{ad}	N	0.030	0.011	2.765	0.014	0.338
P_{ad}	F	0.082	0.067	1.226	0.239	0.091
P_{ad}	$e(P_{ad})$	0.550	0.102	5.410	<0.001	0.661
$e(P_{ad})$	$e(P_{juv})$	-1.337	0.344	-3.881	0.001	0.501
Altitude	Manoeuvrability	0.126	0.257	0.489	0.632	0.016
Night activity	Manoeuvrability	-0.049	0.238	-0.204	0.841	0.003