

Paper IV

1 **Breeding persistence of Slavonian Grebe (*Podiceps auritus*) at long-term monitoring sites:**
2 **Predictors of a steep decline at the northern European range limit**

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25 Abstract

26 The Slavonian Grebe (*Podiceps auritus*) has its European northern range limit in northern Norway and
27 is a species of national conservation concern due to its small population size and unknown
28 population trend. Long-term monitoring at the range limit suggests breeding site use is in decline.
29 We used annual occupancy data from 104 breeding lakes monitored since 1991 in northern Norway
30 to investigate correlates of change in occupancy. Persistence was 100 % until 1999, but thereafter
31 decreased to 25 % (26 lakes with breeding pairs). A particular steep decrease occurred between
32 2010 and 2012. Persistence increased with the number of pairs present in each lake in the initial
33 monitoring year of 1991. The number of grebe pairs also decreased in the lakes that had continuous
34 breeding persistence over the entire 22-year monitoring period, suggesting a large-scale factor
35 caused the population decline. Over the last year of the monitoring series, lake altitude was
36 negatively related to the probability of persistence, indicative that harsh climate played some role.
37 The temporal pattern of persistence was not related to mean winter temperature, however the
38 decrease between 2010 and 2011 coincided with a late ice melt in 2010. Monitoring that includes a
39 larger area of the species' range is required to conclude whether the observed decline indicates an
40 overall decline in population size or range fluctuations at the edge of the species' range. However,
41 investigating the processes that determine population range borders can give insights into important
42 limiting factors pertinent to the conservation of species in the long term.

43

44 Key-words:

45 range change, red list, conservation, proportional hazard models, long-term monitoring

46 **Introduction**

47 Identification and management of species of conservation concern is hampered by a lack of
48 knowledge about the population trends of the target species. Knowledge is often dependent on
49 species' popularity with both knowledge of population trends and conservation management being
50 most prevalent for birds, butterflies and mammals and less so for other insects and amphibians (Lecis
51 and Norris 2004, van Swaay et al. 2008). Even for charismatic species, monitoring to capture spatial
52 variation in population trends and ranges is often lacking. However, in recent years more robust
53 monitoring programs have been established that allow estimation of change in nation or continent-
54 wide population ranges (e.g. Newson et al. 2005, van Swaay et al. 2008, Thomas 2010).

55 Site and/or habitat occupancy may vary temporally and spatially, with occupancy at range edges
56 especially prone to change over time as the ecological conditions are at the limits of those under
57 which the species is adapted to exist (White 2008, Sexton et al. 2009, Gilman et al. 2010, Rius and
58 Darling 2014). Thus, (sub-)populations at species range edges are often transitory (Lawton 1993),
59 existing in metapopulations or source-sink populations (Hanski and Gaggiotti 2004) which can be
60 reduced to extinction state when conditions become less favourable.

61 Investigating causes of change in species range has received much attention in the scientific
62 literature particularly with respect to climate change and its implications for vulnerable species (e.g.
63 Chen et al. 2011, McClure et al. 2012). Physical factors (e.g. climate) are recognised as being the
64 principal drivers of species ranges at regional and larger scales, whereas biological interactions are
65 more important at local scales (Araújo and Luoto 2007). In addition, physical factors are considered
66 to be of primary importance at northern species' ranges, although some advocates of climatic
67 envelope models state the need for the inclusion of demographic factors such as dispersal and
68 intra/interspecific interactions (e.g. Davis et al. 1998). Demographic factors may be of particular
69 relevance for species characteristically breeding in small numbers in discrete habitat patches across
70 their range with the small unit size making patches prone to extinction due to founder effects and
71 demographic stochasticity (Traill et al. 2007, Moran and Alexander 2014, Rius and Darling 2014).
72 Species that migrate between breeding and non-breeding grounds may moderate the risk of patch
73 extinction by forming seasonal re-colonising waves (Moran and Alexander 2014). As such, migratory
74 species have the potential to exist in suboptimal breeding areas.

75 Empirical studies involving both physical and biotic correlates of range change can result in important
76 insights into decisive factors underlying range shift (e.g. Lecis and Norris 2003, McClure et al. 2012)
77 and are therefore an essential component for guiding effective management for species of
78 conservation concern. Much data is readily available from existing databases regarding site

79 characteristics of high biological significance for species. Combined with existing temporal site
80 persistence data, this can be used to investigate decisive factors for range shifts.

81 Slavonian Grebe (*Podiceps auritus*), is a species of national conservation concern (Kålås and Viken
82 2006, Direktoratet for naturforvaltning 2009), however there is currently no systematic monitoring at
83 the national scale (Øien and Aarvak 2008). The Slavonian Grebe is a seasonally migratory species,
84 overwintering in coastal regions and breeding in small numbers mostly on small inland lakes (Faaborg
85 1976, Sonntag et al. 2009, Summers et al. 2011). Present in Northern Norway at the northern end of
86 its European range for over a century, the species experienced an apparent increase in numbers
87 between the 1970's and 1990's (Fjeldså 1973a, Strann and Frivoll 2010). However, monitoring of
88 active northern breeding sites from the 1990's to present shows a decrease in number of pairs and
89 site use (Strann et al. 2014). At the southern end of its Norwegian range it is becoming more
90 abundant and it appears to be spreading southwards (Øien and Aarvak 2008). Proposed but largely
91 untested factors responsible for the decline of the Slavonian Grebe have been identified in an action
92 plan for the species (Direktoratet for naturforvaltning 2009) and include predation by mink (Stien and
93 Ims 2015), predation by corvids and food resource competition with fish. However, additional factors
94 including several habitat characteristics expected to have biological significance as drivers of site
95 persistence and indeed range change were not included.

96 We investigated the breeding site persistence of Slavonian Grebe at 104 lakes at the northern edge
97 of its population range between 1991 and 2012 in order to evaluate the relationship between
98 pertinent physical and biological factors and the population decline. We expected lakes with small
99 populations, unproductive habitat and harsh climate to be more prone to perish. We discuss the
100 implications for management of this targeted species from the study.

101

102 **Materials and Methods**

103 **Study species and area**

104 **Study species**

105 The Slavonian Grebe, hereafter referred to as grebe, has a circumpolar distribution mainly at 50 – 65
106 °N in the boreal climatic zone, breeding in North America, Europe and with isolated populations in
107 Iceland, Færoes and Scotland (Bird Life International 2011). In Norway, the species extends between
108 60° 52' and 69° 30' and so forms one of the most northerly ranges for the species internationally
109 (Fjeldså 1973a, Fournier and Hines 1999). Occasional breeding has been recorded further north in

110 Norway in eastern Finnmark and adjacent districts in Finland and Kola Peninsula (Fjeldså 1973a). The
111 populations of Norway, Iceland and Scotland are described as a subspecies *P.a.arcticus*, being
112 morphometrically semi-distinct and are thought to have different origins from the rest of the
113 Western European population (Fjeldså 1973a).

114 The grebe spends most of the year in marine habitat but migrates inland to breed between May and
115 September. Breeding can occur in both freshwater and brackish water and in a wide range of lakes
116 sizes, with sites (< 10 ha) common in north America and the Baltic and a larger range of site area
117 used in northern Norway and Iceland (Fjeldså 1973b, Faaborg 1976, Ulfvens 1988, Ewing et al. 2013).
118 Sites commonly have between 1-2 pairs and seldom more than 20 pairs per lake (Fjeldså 1973c,
119 Faaborg 1976). In Norway, winter habitat is in coastal archipelago and outer fjord systems (Fjeldså
120 2004, Strann and Frivoll 2010) with part of the population migrating as far south as the Scottish coast
121 (Øien and Aarvak 2009). Inland observations during winter are rare and are normally before ice has
122 formed on lakes or on ice free lakes close to the coast (Cramp et al. 1977, Øien and Aarvak 2008).
123 Onset of nest building is determined by ice melt and varies considerably with latitude, altitude and
124 season (Cramp et al. 1977, Fjeldså 2004). Nests consist of floating rafts of dead plant material,
125 constructed in shore vegetation. Diet during the breeding season consists mostly of fish by biomass
126 but also of aerial and aquatic invertebrates (Fjeldså 1973b, Dillon et al. 2010). Young and adults
127 migrate to the coast in September.

128 The species has a circumpolar population of 140,000 - 1,100,000 individuals (Bird Life International
129 2011). The general trend for the population is declining e.g. 75 % decline in North America over the
130 last 40 years (Bird Life International 2011), but due to the size and geographical extent of the
131 population, the species is categorised as 'least concern' on the IUCNs red list. In Western Europe and
132 Scandinavia, historical records indicate a range expansion westward into southern and middle
133 Sweden during the late 1800's and early 1900's. The populations in northern Norway and Iceland
134 have been in existence for at least 2 centuries while the population in Scotland established itself
135 during the first half of the 20th century (Fjeldså 1973a, Douhan 1998). In Norway (Figure 1), historical
136 records indicate that the core area in the 1970's was between Bodø and mid Troms and was
137 estimated to be c. 400 pairs (Fjeldså 1980).

138 Although no systematic monitoring of grebe occurs on a national scale, regional scale monitoring of
139 core sites in Troms and bordering Nordland reveals a decrease in the use of breeding sites compared
140 to when monitoring began in 1991 (Strann and Frivoll 2010, Strann et al. 2014). National declines
141 have been reported in neighbouring countries with an estimated 54% decline between 1972 and
142 1996 in Sweden (Douhan 1998) and strong negative population change index since 1997 in Finland

143 (Pöysä et al. 2013). In Sweden, the population appears to have increased again and in 2011 was
144 estimated to be close to the 1972 estimate of 2200 pairs (Norevik 2014). This increase has been an
145 accompanied by an apparent eastward shift in its range away from inland areas to areas along the
146 Swedish Baltic coast (Norevik 2014).

147 **Study area**

148 We report data from 104 study sites located in Troms and northern Nordland regions, between
149 68°30' and 69°43' N and 16°39' and 22°09' E. Sites were chosen for monitoring annual breeding
150 success and were therefore all occupied in 1991. Six sites were omitted from the analysis as they had
151 very different habitat characteristics than those of lakes; five occurred in "lombolas" which are small
152 widenings of river sections and one opened directly into the sea. The 104 study sites were all inland
153 and fed by streams or rivers and/or had rivers as outflows. Average (mean) water body area was 93
154 ha (median 19.18, range 0.34 – 1521 ha) and mean altitude was 90.98 m (median 91.00, range 0-269
155 m). Immediate surrounding vegetation was dominated by mosaics of mountain birch (*Betula*
156 *pubescens*), Scots pine (*Pinus sylvestris*), mire, heath and grassland. Agricultural grassland also
157 existed around some lowland lakes. Lake bedrock consisted of mostly calcareous rock types including
158 mica, mica slate, meta-sandstone and amphibolite, with smaller frequencies of marble rock types
159 including calcareous mica and marble. Granite rock types including dioritic to granitic rocks and
160 conglomerate and breccia occurred less often. Lakes were mostly oligotrophic with several
161 mesotrophic and eutrophic lakes. Dominant shallow water vegetation included bottle sedge (*Carex*
162 *rostrata*) and to a lesser extent bogbean (*Menyanthes trifoliata*), and provided nesting habitat for the
163 grebe. Lake vegetation was sparse in oligotrophic lakes forming small pockets of nesting habitat, and
164 more or less continuous in eutrophic lakes, providing continuous nesting habitat around the lake
165 edge perimeter. Mean distance from lake centroids to nearest road, ranging from district to
166 European road, was 0.53 km (median 0.44, range 0.25 – 1.99 km).

167

168 **Data**

169 *Grebe monitoring*

170 Monitoring was based on two visits each year in the period 1991-2012. The first visit was around 22
171 June, roughly 3 weeks after ice melt and the second between 10 and 20 July (exceptionally the end of
172 July). Number of nesting pairs, territorial pairs and non-territorial individuals were counted in both
173 visits from standardised observation points using binoculars and telescope. The counts of nesting

174 pairs were used in the analysis and were expressed as a single unit of observed number of breeding
175 pairs per lake in the analysis.

176

177 *Habitat*

178 Habitat variables were extracted using ArcMap 10.0. Lake bedrock was categorised into three
179 bedrock categories, calcium, granite and marble to reflect water pH and hence be a proxy for lake
180 ecosystem productivity determining nesting habitat and food resource availability. Marble category
181 was used where marble derived bedrock was present, calcium category where calcareous bedrock
182 was present in the absence of marble, and granite category where bedrock was derived of granite
183 without the presence of marble or calcium. Vegetation around each lake was classified based on a
184 national vegetation map developed from Landsat imagery (Satveg, Johansen 2009). From this map
185 the original 25 vegetated classes were grouped into 6 initial habitat types: coniferous forest,
186 deciduous forest, mire, alpine, herb and agriculture and further into three broad landscape types:
187 forest, open lowlands (mires, herb and agriculture) and alpine. The proportion of the different
188 habitat types were calculated in two buffers surrounding each lake with a radius of 100 m and 200 m
189 respectively. Visual inspection of the resulting proportions revealed no difference between the two
190 buffer radii and a 100m buffer was therefore chosen to represent the proportional coverage of
191 habitat and landscape types around each lake. Proportion of agricultural land was used as a proxy of
192 eutrophication which has been shown to be associated with colonisation of previously unused
193 breeding areas (Douhan 1998). Distance between individual lakes and nearest road was used as a
194 proxy of disturbance.

195 As no data existed for the date of ice melt of individual lakes, we explored the use of air surface
196 temperature and snow depth data as possible proxies (Borgstrøm et al. 2010, Kvambekk and Melvold
197 2010, Godiksen et al. 2012). Values were extracted from national air temperature and snow depth
198 models with a 1 km grid resolution (<https://met.no>). Where lakes crossed two grid squares, the
199 value from one of the grid squares was used, selected at random. Mean temperature and total
200 cumulative positive temperature (°C) were expressed as yearly mean and yearly summed
201 temperature > 0 °C respectively for time-dependent analysis (see below) and total mean and total
202 positive cumulative temperature for the time-independent analysis. Snow depth was expressed as
203 yearly mean snow depth or total mean snow depth. Exploration of three winter time periods 1st
204 November – 31st May, 1st January – 31st May and 1st April – 30th June indicated that ice melt was best
205 indicated by positive cumulative temperature and that there was no statistical difference between
206 time periods (AICc, Burnham and Anderson 2002). The period January – end of May was used with a

207 sample size of 99 lakes for the time dependent-analysis of ice melt as five lakes shared
208 meteorological data grid squares.

209 **Statistical analysis**

210 The key response variable was grebe site persistence (hereafter persistence). This variable was taken
211 as the number of years from the onset of the monitoring to the year grebes disappeared from the
212 site or until the end of the monitoring series in case grebes continued to be recorded during the
213 entire 22 year monitoring period (i.e. until 2012). The presence-absence records indicated that
214 detection rates were very high as continued presence were interrupted by one (n=11) to two years
215 (n=2) in only 13 of the 104 lakes. Thus detection rate could be assumed to be close to unity (and thus
216 omitted from the analysis) which allowed for more flexible and powerful analyses by semi-
217 parametric Cox proportional hazards models (R library survival). For the 13 lakes with pseudo-
218 extinctions the intermittent zeros (absences) were replaced with ones (presence) in those data
219 records. The Cox proportional hazards model estimates the instantaneous risk of an event
220 happening, in this case cessation of use of lake as breeding habitat and takes the form

$$221 \log h_i(t) = \alpha(t) + \beta_1 x_{i1} + \beta_2 x_{ik} + \dots + \beta_k x_{ik}$$

222 where $h_i(t)$ is the hazard function i.e. the instantaneous risk of loss of breeding lake at time t , given
223 the survival to that time, $\alpha(t)$ is an unspecified baseline hazard function and $\beta_k x_{ik}$ are the covariates
224 entered into the model linearly (Fox 2002).

225 The full model contained additive effects of the continuous predictors altitude, lake area, number of
226 breeding pairs at t_0 (i.e. 1991), distance to nearest road (road) and proportion of agricultural land
227 (vegetation) and the 3 level factor bedrock with classes marble, calcareous and granite. The number
228 of breeding pairs was used as a proxy for susceptibility to demographic stochasticity which could be
229 expressed as total mean, total maximum and number at start of monitoring in 1991 (t_0). These
230 indices of local population size were highly correlated but investigation showed that number of pairs
231 at t_0 was the best predictor. Ice melt was initially explored as a time-dependent variable but the
232 coefficient estimate was not significant. Ice melt was therefore entered as a time-independent
233 variable in time-independent Cox proportional hazard model. As ice melt and altitude were highly
234 correlated, the two were entered in separate models. All continuous variables were transformed to
235 centralise their distributions and increase linearity, with square root transformation for altitude,
236 number of breeding pairs (t_0), road and agricultural land. Lake area was log-transformed. Analyses
237 were carried out in software package R (R Core Team 2014) and best model chosen by AICc.
238 Goodness of fit of the selected models were assessed by Chi square test on Schoenfeld residuals.

239

240 **Results**

241 The model including effects of altitude, lake area and number of breeding pairs at t_0 best predicted
242 the persistence of breeding sites. However, this model showed violation of the assumption of
243 proportional hazards for both altitude (Schoenfeld residuals $\chi^2 = 6.19$, $P = 0.01$) and number of
244 breeding pairs at t_0 (Schoenfeld residuals $\chi^2 = 10.56$, $P = 0.0001$). Examination of the residual plots
245 suggested that the hazard ratios increased abruptly for these predictors between 2011 and 2012.
246 We therefore split the data into 2 groups to be analysed in separate models with the same
247 covariates; the first model for the period 1991-2011 and the second for 2011-2012. As the second
248 period had had one time interval, the analysis could be simplified to a binary logistic regression of the
249 probability of one further year persistence of those lakes with breeding pairs still present in 2011.
250 The fit for proportional hazard model containing effects of altitude, lake area and number of
251 breeding pairs at t_0 was good when leaving out the last year of the time series (2012) (Schoenfeld
252 residuals 1991 - 2012: $\chi^2 = 5.72$, $P = 0.12$). Only the coefficient for the predictor *number of pairs at t_0*
253 was statistically significant (Figure 2). The estimate of this coefficient shows that an additional
254 increase of 1 in the square root of number of breeding pairs at time t_0 , reduced the hazard rate for
255 loss of breeding lake by 90.2 % ($\exp[-2.31] = 0.098$, $P < 0.001$). The proportional hazard rate model
256 for the period 1991 - 2011 explained 44 % of the variation and had good predictive power with an
257 AUC of 81 % (95 % C.I. 71 - 89). Mean predicted probability of individual lake persistence after 21
258 years (in 2011) was 0.36 (95% C.I. 0.28 – 0.47). The loss of breeding sites began after 8 years (1999)
259 (Figure 2) with a pronounced additional drop in the probability curve after 20 years (between 2010
260 and 2011). In the logistic regression model for the period 2011 – 2012 only the coefficient for altitude
261 was significant (-0.23 ± 0.10 , $P = 0.02$, area = -0.20 ± 0.28 , $P = 0.48$, number of pairs at $t_0 = -0.07 \pm$
262 0.87 , $P = 0.93$, $df = 34$; Fig. 3). Between 2011 and 2012, mean predicted probability of individual lake
263 persistence decreased by 31.6 %.

264 None of the habitat variables except altitude and lake area predicted the persistence of grebe in
265 individual lakes. There was a small significant negative correlation between number of breeders at t_0
266 and proportion of mire (-0.27 , $P = 0.005$) and small significant positive correlation between number
267 of breeders at t_0 and the proportion of herbs (0.31 , $P = 0.001$), which to some extent might have
268 concealed their effects. Goodness of fit test revealed that the overall model containing ice melt
269 showed some indication of violation of the assumption of constant proportional hazard of predictor
270 variables ($\chi^2 = 15.00$, $P = 0.03$), with both number of pairs at t_0 and ice melt showing indications of
271 being non-proportional in predicting hazard rate ($P < 0.05$). As model selection using AICc showed no

272 difference between the use of altitude or ice melt, altitude was used, enabling the use of all 104 sites
273 in the analysis.

274

275 **Discussion**

276 The present 21-year monitoring series of breeding Slavonian Grebe in the northernmost part of its
277 distribution range in Europe showed clear evidence of a decline. The onset of the decline in grebe
278 breeding site occupancy began in 1999 and by 2012 the number of lakes with breeding pairs steeply
279 declined to one quarter of those lakes that had breeding grebes 13 years earlier. The results support
280 our predictions that lakes with small breeding populations, and to some extent poor environmental
281 conditions (high altitude), have lower persistence but do not support our prediction that
282 unproductive habitats lead to lower persistence. Persistence of breeding status was predicted well
283 for the majority of the monitoring period by the inclusion of the variables number of breeding pairs
284 and in the final year of monitoring by altitude. The number of pairs per site at the onset of
285 monitoring in 1991 was also an excellent representation of the maximum number of pairs per site (r
286 = 0.90). Thus, sites with small breeding populations were highly vulnerable to extinction, and the
287 number of breeding pairs in the initial monitoring year explained the majority of the variation in
288 persistence, potentially due to demographic stochastic processes (Caughley 1994). Whether
289 persistence was maintained by site faithfulness by the same individuals over successive breeding
290 seasons or replacement of individuals to the same sites via source-sink dynamics is not known as
291 individuals were not followed in this study. However, evidence from other studies suggests that
292 recruitment from within the regional population at least in part by returning females may well play a
293 role in population persistence. Ferguson et al. (1981) found that individuals return to breeding sites
294 in successive breeding seasons resulting in a certain level of both lake faithfulness and a wider local
295 area faithfulness (Ferguson 1981), while Fournier and Hines (1999) and Ewing et al. (2013) found a
296 positive association between breeding success on population growth rates in the following year. It
297 can be noted that in our study the dominant pattern of lake occupancy was not represented by
298 stochastic extinction- re-colonising dynamics at site level, indicative of classical meta-population
299 dynamics. Rather the situation appears to be more in line with a “declining population paradigm”
300 due to some deterministic driver (*sensu* Caughley 1994). Indeed, an overall steady decline in number
301 of breeding pairs was even evident for those lakes that maintained continuous presence of breeding
302 grebes over the 21 years (Figure 4). A similar declining trend (which has been ongoing since 1993)
303 has occurred in the Scottish population of Slavonian Grebe (Ewing et al. 2013). While this population
304 forms a southern range boundary for the species and may be expected to be sensitive to other

305 processes such as range contraction due to climatic warming (Green et al. 2008), low breeding
306 success appears to be partly responsible for the decline in the Scottish population. Identification of
307 factors that can fully explain the decline have so far eluded research efforts (Ewing et al. 2013).
308 Reasons for the change in numbers and eastern movement of the Swedish population are also
309 currently unknown (Douhan 1998, Norevik 2014).

310 The lack of relationship between breeding site persistence and the meteorological variables (air
311 temperature and snow depth) used here as proxies for ice melt dates may have been due to small-
312 scale topographical variation in temperature and catchment effects (Kvambekk and Melvold 2010)
313 not captured in the meteorological data. It would be useful to have better knowledge regarding the
314 extent to which these variables capture the variation in ice melt times at individual lakes. Site
315 persistence was also not correlated with mean winter temperature. However, the drop in persistence
316 between 2010 and 2011 occurred after an exceptionally late ice melt in 2010. The resulting
317 shortening of the breeding season may have resulted in the observed reduced site use the following
318 year. Lagged effects on reproductive performance are apparent in several avian studies and include
319 site avoidance after poor performance (e.g. Stacey and Robinson 2012, Hanssen et al. 2013). As
320 grebes are income breeders (Kuczynski and Paszkowski 2010), the late breeding onset may have
321 limited quality of eggs and/or offspring resulting in low productivity. Poor body condition combined
322 with migration to wintering grounds, or non-related but correlated factors in wintering areas such as
323 poor weather could have resulted in reduced over wintering survival (Newton 1998, Golet et al.
324 2004, Sandvik et al. 2005, Frederiksen et al. 2008). Altitude also negatively affected grebe
325 persistence but significantly so only between 2011 and 2012. Altitude affects temperature and
326 precipitation and modulates lake productivity and grebe breeding season length (Summers and
327 Mavor 1995). Snow and ice cover delay return dates of individuals breeding at higher latitudes as
328 they do not return to their breeding sites before there is open water (Fournier and Hines 1999, Øien
329 et al. 2008). Presumably, the variation in ice melt day in this study was not sufficient to prevent grebe
330 from initiating a breeding attempt apart from in 2010. In 2012, low altitude sites may have been
331 available to most breeders as site occupancy had become so low. Alternatively, high altitude
332 breeders may have been of poorer quality and so not attempted to breed in 2012.

333 We found no effects of habitat productivity, as indicated by bedrock, or presence of agricultural
334 grassland indicating eutrophication. The majority of lakes in this study had either neutral or alkaline
335 water characteristics based on bedrock classification, thus a water chemistry that should not limit
336 fish growth or invertebrate abundance (Eriksson 1986). In addition, aerial insects make up a large
337 proportion of grebe diet and are unlikely to be limited (Fjeldså 1973b, Dillon et al. 2010). In this
338 study, only 19 of the 104 sites were less than 5 ha. This is in contrast to studies from the Baltic and

339 North America that have reported that the majority of sites were less than 5 ha but in common to
340 earlier studies in northern Norway (Fjeldså 1973c, Faaborg 1976, Summers et al. 2011). The lack of
341 relationship between lake area and breeding number in year t_0 may be modified by variation in patch
342 quality making overall lake area a poor predictor of breeding population size (Hanski and Gaggiotti
343 2004, Lenda and Skórka 2010, Williams 2011). In many of the lakes, overall nesting habitat is patchy
344 and not proportional to lake area. The relationship is further modified by territorial behaviour of the
345 grebe, making high densities unlikely unless vegetation suitable for breeding is abundant (Fjeldså
346 1973c, Faaborg 1976).

347 The distribution and numbers of grebe present in the initial monitoring year (1991) suggests a
348 possible recent northern increase in the species range compared to historical accounts gathered
349 between the 1950's and early 1970's (Fjeldså 1980, Strann et al. 2014, Fjeldså pers. comm.).
350 Although the mechanisms behind this shift are unknown, the present study indicates that range
351 expansion further north has probably been limited by climatic conditions even though there is plenty
352 of available habitat. We are not aware of any published data on the range dynamics at the northern
353 end of the North American range during the same period, however a study of grebe towards the
354 current North American range edge by Fournier and Hines (1999) shows a clear pattern of population
355 growth with both temperature, precipitation and ice free days. The amount of mixing between the
356 Swedish population and the Norwegian population is unknown but thought to be little (Fjeldså
357 1973a). Future investigation of the existing study population's overwintering movements may help
358 determine whether the change is due to reduced mortality or use of alternative breeding sites.

359 The grebe is suffering decline in both its North American and western European range. In Norway, it
360 now appears to be declining at the northern end of its range. This decline is mostly associated with a
361 low number of pairs at most sites making the grebe very vulnerable to site extinction, in particular in
362 harsher (higher altitude) environments. In order to say whether this reduction is indicative of a wider
363 decline in the population, it is necessary to expand monitoring to cover a spatial extent that allows
364 estimation of grebe population trends. Optimally, combining spatial data together with data on vital
365 rates, site faithfulness, individual dates of ice melt and habitat characteristics measured at site scale,
366 will allow us to come closer to understanding the main population drivers are in the grebe population
367 and whether they are manageable by human intervention.

368

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374

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505 Figure 1. The historical Norwegian distribution of Slavonian grebe between 1950 and 1970 adapted
506 from Fjeldså (1973a) and the distribution for the present study between 1991 and 201. The historical
507 distribution is located in northern Nordland and Troms (A), Helgeland coast (B) and North Trøndelag
508 (C) and the sites used in the present study are shown by dots.

509

510 Figure 2. Predictions (solid lines) of probability of grebe breeding persistence with 95% C. I. (dotted
511 lines) from the best model for Cox proportional hazard model for 104 lakes in Troms and northern
512 Nordland for the period 1991-2011 a) mean of all co-efficient estimates, and predictions for
513 different levels of b) number of pairs (t_0), c) lake altitude and d) lake area. P-values are derived from
514 z-test of the coefficients of the predictor variables.

515

516 Figure 3. Predicted effect of altitude in time-period 2011 and 2012. The estimate is derived from a
517 logistic regression model with altitude as the back-transformed predictor of site persistence. 95 %
518 C.I. are shown with dotted lines and the observed survival for lakes over the range of altitudes are
519 shown with open circles. The figure is shown with the full range of altitude values.

520

521 Figure 4. Mean number of breeding pairs per site and their standard deviations for the 26 sites that
522 still had presence of breeding pairs in 2012.

Figure 1.

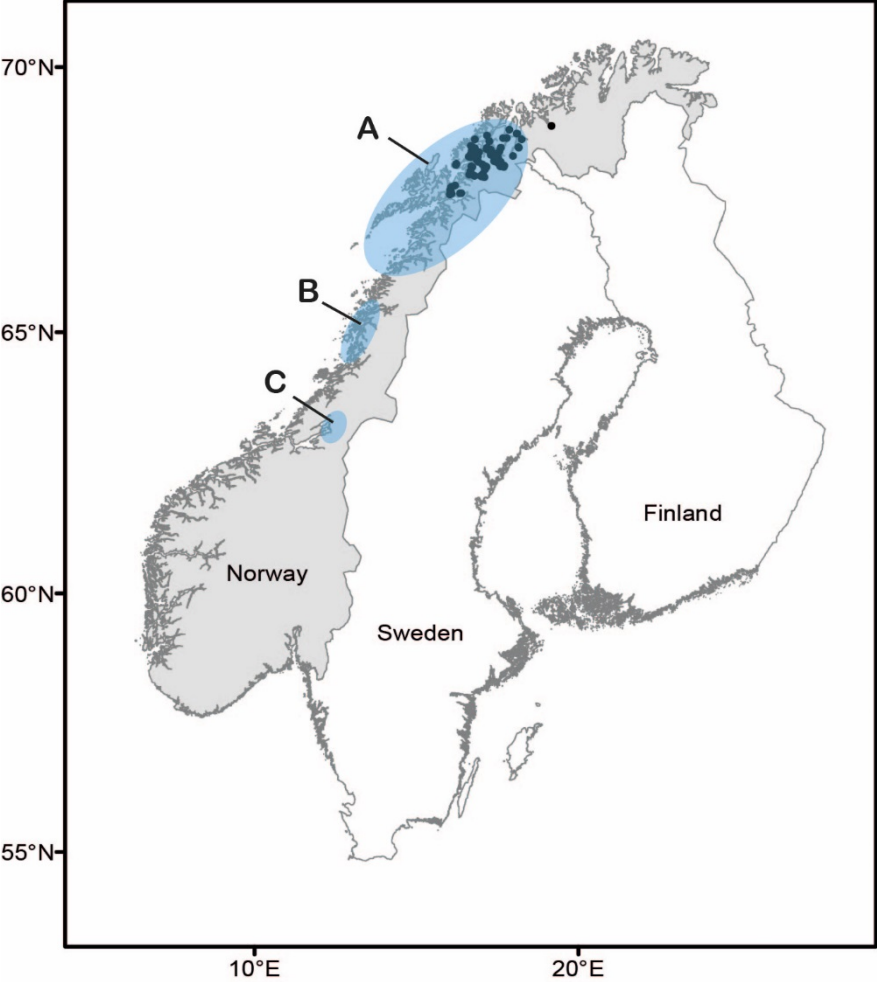


Figure 2.

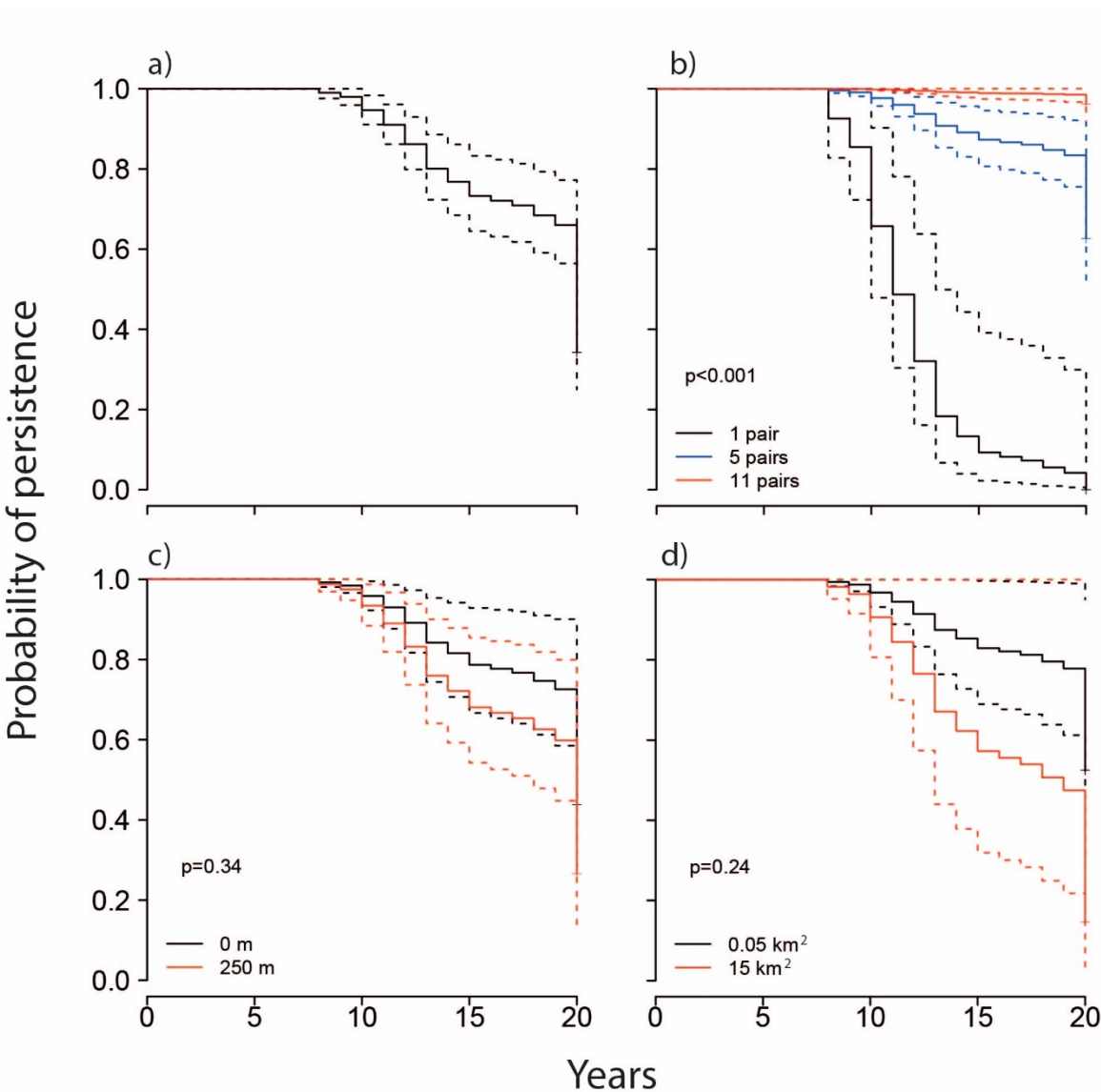


Figure 3.

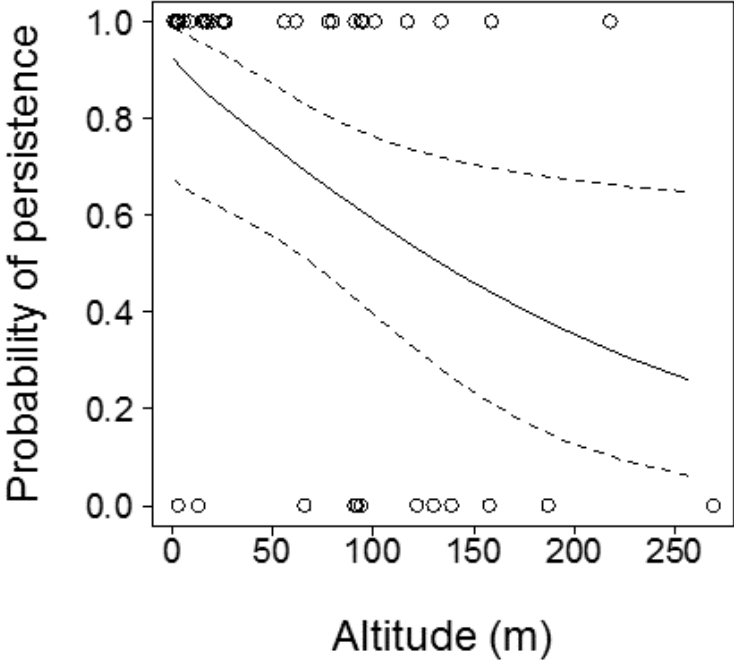


Figure 4.

