1 **Population recovery of peregrine falcons in central Norway in the four decades since the DDT-**

2 **ban.**

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10 **Abstract**

11 The breeding population of peregrine falcons (*Falco peregrinus*) in Norway was almost exterminated by the

12 early 1970's. Long-term monitoring of breeding pairs has been conducted since 1976 up to present. Peregrine

13 falcons were first established at breeding sites in coastal habitats, where they remained at stable low numbers

14 until the early 1990's. Starting around 2000, numbers began to increase steadily, and current numbers have now

15 reached historical population levels from the pre-DDT era. We documented a range expansion with increasing

16 numbers of peregrines nesting in the fjords and inland valleys. We found that once a territory was colonized, the

17 probability that a territory remained occupied was high ($S > 0.958$). During early stages of population recovery,

18 the transitional probabilities of becoming or remaining a breeding territory were high ($\psi_{N-B} > 0.40$, $\psi_{B-B} > 0.65$)

19 but declined over time, especially in coastal habitats. Moreover, the productivity per nest has also decreased

20 over time at sites in coastal habitats in the former stronghold of the population. The levels of environmental

21 pollutants in eggs of the peregrines have dropped sharply over the last few decades, and contaminant levels now

22 seem to be below critical levels. Eggshells were relatively thin throughout the 1970s, 1980s, and 1990s, but have

23 increased to almost normal levels during the last two decades. Reductions in levels of organochlorine pollutants,

24 especially DDT, appear to have been the main factor in explaining the population recovery. The territory

25 dynamics are consistent with density-dependence and the low breeding success of the coastal-breeding

26 peregrines is believed to be caused by declining numbers of colonial seabirds and other prey species.

27 **Keywords**: eggshell thickness, environmental pollutants, population model, population recovery, prey decline

28 **Acknowledgments**

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Introduction

The historical population of peregrine falcons in Norway was estimated to have been 500-1,000 pairs before the introduction of DDT (Dichlorodiphenyltrichloroethane) as an agricultural chemical (Schei 1984). Elsewhere in Fennoscandia, population numbers were estimated to have been around 1,000 pairs in Finland (Linkola and Suominen 1969), while the historical population was estimated to have been 900-1,400 pairs in Sweden (Lindberg et al. 1988). By the mid-1970s, no more than eight localities with breeding pairs of peregrine falcons were known in the whole of Norway (Lindberg et al. 1988). In Denmark, the last known breeding attempt was in 1972 (Andreasen 1972), and in Sweden only nine remaining pairs were believed to survive by 1974, three pairs were known to breed in the southern part of the country, and 5-6 pairs in the northern areas of Lapland by 1974 (Lindberg 1975). In Finland, only 15 territories were occupied in 1965 (Linkola and Suominen 1969). Steep population declines led to serious concerns that the peregrine falcon was about to be eradicated from Fennoscandia, as it had happened elsewhere in the world, such as in the eastern parts of the United States (Hickey 1969).

After World War II, the world was slowly becoming aware of new and severe threats to bird populations. Predatory species at high trophic levels were especially susceptible to exposure to pollutants, especially by the massive use of pesticides such as DDT and dieldrin in agricultural production. The first documentation of thin-shelled eggs in nests of peregrines in Britain was published in 1958 (Ratcliffe 1958). The book 'Silent Spring' by Carson (1962) had made the whole world aware of the danger posed by DDT and other pollutants on wildlife, especially birds of prey. It still took about 20 years before the main reason for population declines was pinpointed. The mechanism of eggshell thinning caused by DDT (or rather by one of its degradation products, DDE, Dichlorodiphenyldichloroethylene), and eggshell-thinning was later established (Lundholm 1987; Peakall et al. 1975; Ratcliffe 1967, 1970), but also adult mortality caused by pesticides in the cyclodiene group (dieldrin and endrin) was probably important (Bogan and Mitchell 1973; Nisbet 1988; Porter and Wiemeywer 1969). The use of alkyl mercury in the agricultural areas of Scandinavia may also have contributed to increased mortality and hatching failures (Lindberg and Odsjö 1983). The process of bioconcentration and biomagnification through food-chains allowed relatively low environmental concentrations to reach high levels in predatory species at high trophic levels (Braune et al. 1988; Fisk et al. 1998; 2003). Norway and Sweden banned the use of DDT as an agricultural chemical in 1970.

The goal of our study was to monitor the recovery of a local population of peregrine falcons in central Norway, in parallel with a broader effort to study the magnitude and effects of environmental pollutants across Norway, to see whether pollutants were having an effect on a population level. We conducted intensive surveys of falcons at a regional scale in Trøndelag, whereas collection of eggs for monitoring of environmental pollution was conducted at a national scale as part of the long-term Monitoring Programme for Terrestrial Ecosystems (TOV) (Gjershaug et al. 2008). We use the pollutant load of falcon eggs in Norway as index of long-term changes in contaminant exposure for our local population. We also wanted to document a population expansion into new habitats (fjord and inland) as it became clear that the breeding distribution was shifting over time. Here, we report on the population recovery and territory dynamics of peregrine falcons in central Norway over the past four decades.

Methods

Field work. We monitored the population status of peregrine falcons in central Norway (63°30' N - 65°N, Figure 1) for a 42-year period during 1976-2017. Our study area was the former Nord-Trøndelag county, part of Trøndelag county since 2018. Only sites from within the boundaries of former Nord-Trøndelag county were included in our study (22,412 km^2). Suitable nest sites in the breeding territories were surveyed 1-4 times during the summer breeding seasons for the 42-year period from 1976 to 2017. From 1976 to 2011, all known territories were surveyed, but from 2012 to 2017, surveys of 1-4 territories were skipped each year, due to their long history of being abandoned. Nest sites were confined to cliff faces or rocky escarpments in three different habitats: coast, fjord and inland sites. Coastal habitats were defined as sites situated adjacent to the Norwegian sea. Fjord habitats were sites in long narrow fjords that were perpendicular to the outer coastline, mainly the Trondheimsfjord. Inland habitats included terrestrial sites and mountain valleys, at least 10 km away from fjord or the sea. Breeding pairs sometimes moved a short distance to a new nest site, but we considered an area to be the same territory if adjacent nest sites were in the same cliff or section of neighboring cliffs with no other pair known in the same area. We developed encounter histories for each falcon territory where we coded our annual records as 1 of 4 states: *not surveyed* (.), surveyed but *no falcons* were detected (0), territory was occupied by *nonbreeders* without any evidence of nesting (*N*), or the territory was occupied by *breeders* with confirmed evidence of a nesting attempt containing eggs or young (*B*). Territories coded as occupied by nonbreeders were a heterogeneous group of birds with uncertain status, including sites visited by prospecting birds, unmated birds defending a territory, mated pairs that failed to produce a clutch, or possibly pairs with nests that failed at an early stage of the breeding attempt. Uncertainty in state determination can be addressed with multistate occupancy models in a robust design framework (Nichols et al. 2007), but we did not use this approach because territory status was coded by year and not by survey visit in our long-term monitoring program.

Mark-recapture models. We modeled the territory dynamics of falcons with multistate mark-recapture models in Program Mark (ver. 6.2, www.phidot.org/software/mark). We were unable to test for overdispersion because our encounter histories included sites that were not surveyed. We assumed that overdispersion was low and used Akaike Information Criterion (AICc) for model selection. Our data were sparse because population numbers remained low during the first 22 years of our study period and then grew slowly during a 20-year recovery period. Models with full time-dependence were not possible because falcons colonized the three different habitats (coastal, fjord and inland) at different times and not all transitions were identifiable. We opted for a starting model where the probabilities of territory persistence (S_N and S_B) and encounter (p_N and p_B) were estimated separately for the two different states (*N* or *B*), but were held constant over time and among habitat strata. We modeled the transitional probabilities of changing states (ψ_{N-B} and ψ_{B-N}) separately by state, as a linear trend over time, and as a group effect of the three different habitats (coast, fjord, and inland sites). We considered single factor models, main effect models (+), and factorial combinations (×) of the two explanatory variables. We ranked models by differences in information criterion values (ΔAICc) and used ratios of Akaike weights to assess relative support for alternative models. In a last step, we used model averaging to calculate estimates with unconditional variance that controlled for uncertainty in model selection. To compare transitional probabilities to a breeding state, we calculated the probability of territory persistence for breeders as: $\psi_{B-B} = 1 - \psi_{B-N}$.

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Population change. Our multistate models provided state-specific estimates of the probability of encounter, which were sometimes less than one. Accordingly, the total number of falcon territories during the starting and ending year were estimated from territory counts (*C*) corrected for the state-specific probabilities of encounter (*p*): $\hat{N} = C_N / p_N + C_B / p_B$. An annual estimate of the mean finite rate of population change (λ) was then estimated as the geometric mean of the population size at the start ($\hat{N}_1$) and end ($\hat{N}_{T+1}$) of a time series that was *T* years in duration: $\lambda = \left(\hat{N}_{T+1} / \hat{N}_1 \right)^{1/T}$. We calculated annual rates of population growth for each of the three habitats, and also for the entire population. Given the observed rates of population growth, we also calculated the doubling time for falcon populations as $T_d = \ln(2)/\ln(\lambda)$.

Pesticides and mercury. Addled eggs that failed to hatch were collected whenever available, and the contents were kept frozen at -21°C before being shipped to the laboratory at Norges Veterinærhøgskole (The Norwegian Veterinary College, Oslo). The laboratory is accredited in compliance with NS–EN ISO/IEC 17025 (TEST 137). The laboratory methods for analyzing chemical content were modified and improved over the 40-year period, and the equipment and procedures are described in detail by previous authors (Berger and Haukås 2005; Frøslie et al. 1986; Holt et al. 1979; Murvoll et al. 2006; Nygård and Polder 2012; Polder et al. 2008; Polder et al. 2008). During the first years, only sum-DDTs were reported. Later, the breakdown products such as DDEs and DDDs were also reported. The p,p'-DDE was always the dominating compound. During later years, a whole array of compounds were analyzed, including HCB, HCHs, mirex, polybrominated compounds (PBDEs) and polyfluorinated compounds (PFAS). Sample size of eggs were relatively small and estimates are available all of Norway but not for individuals or populations. For details of pollutant data from recent years, see Nygård and Polder (2012).

The whole dataset included 183 eggs and eggshell fragment collections from 117 clutches, including the historical eggs that were used as reference for eggshell thickness. Fifty-five eggs from 49 clutches were used for pesticide analysis. Clutch averages were used for statistical purposes and graphs. Addled eggs that that are left abandoned in the nests will lose some of their water content due to evaporation through the eggshell. Water-loss will influence the measured values of pollutant concentration expressed on a wet weight basis. Therefore, we have corrected for potential water loss by recalculating the pollutant concentration values based on mass of a fresh egg without water loss, after estimating egg volume from egg measurements following methods of Helander et al. (2002).

Eggshell thickness and eggshell index. The emptied eggshells were dried, and their mass, length and breadth were measured. In cases where only eggshell fragments were collected from nests, shell thickness was measured with a micrometer designed to measure eggshells (+/- 0.01 mm, Starrett model 1010). The micrometer instrument was also used to measure the shell thickness of whole eggs through the blow-hole (average thickness of four measurements in opposite directions). In absence of addled whole eggs in the nests, eggshell fragments were collected where available. Up to ten fragments from each nest were collected, and their average thickness was used as representative estimate for the clutch. Only fragments containing eggshell membrane were used. All eggshell measurements were made by the first author TN. The eggshell thickness index (SI) was calculated by using the formula SI = mass of eggshell/length×breadth^2 (Ratcliffe 1967), with corrections for hole size and

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150 eccentricity of egg shape (Nygård 1999). Baseline values of egg dimensions before the introduction of

151 organochlorine pesticides were measured for egg sets collected before 1947, that were archived at six natural

152 history museums in Norway (Oslo, Trondheim, Bergen, Kristiansand and Tromsø) and Denmark (Copenhagen).

153 **Results**

154 *Population history*. Peregrine falcons were probably extirpated from central Norway (Nord-Trøndelag and Sør-

155 Trøndelag) during the 1960s, and up until the first pair was discovered breeding at a coastal cliff in Nord-

156 Trøndelag in 1976. Two additional pairs were discovered before 1980, and these three pairs were the only known

157 breeding birds in Nord-Trøndelag for many years, all occurring at coastal sites. No population increase was

158 evident until the mid-1990s, despite considerable search effort (Figure 2). Starting in 2000, a gradual increase

159 occurred, and peregrine falcons have been recorded breeding at 36 different sites in Nord-Trøndelag county

160 during the 42-year monitoring period. Peregrine falcon numbers remained low for the first 22 years of our study

161 period. Colonization of habitats other than the coast was staggered, and falcons first appeared in the fjords in

162 2004, and at inland breeding sites in 2006. Falcons occupied 1-2 territories for the first eight years from 1976-

163 1983, and then 3-6 territories from 1984-2000 (Figure 2). Population numbers began to increase more at the turn

164 of the millennium and went from 9 to 26 yearly active territories during 2001-2017, at altogether 51 sites.

165 Nesting territories, where breeding has been recorded at least once, are at present located in three different

166 habitats: coastal (1976-2017, n = 20), fjords (2004-2017, n = 16), and inland sites (2006-2017, n = 15). About

167 two-thirds of previously active territories were occupied by breeding pairs during 1976-2000 (median 67%,

168 range 0-100%). After the onset of population growth, about half of previously active territories were occupied

169 by breeding pairs during 2001-2017 (median 48%, range 32-89%) (Figure 3). The reproductive rate has varied

170 greatly throughout the years, but average productivity has declined from 2.3 to 0.5 fledglings per pair over four

171 decades in the coastal population (linear regression: fledglings = 79.4 - 0.04×year, P = 0.001, R^2 = 0.256), while

172 there have been no significant trends for changes in productivity in the fjord or inland populations (Figure 4). A

173 tendency for an increase in productivity in the inland population was non-significant, but requires continued

174 monitoring to determine future trends.

175 *Model selection*. Our multistate modeling of territory dynamics was based on encounter histories from 51

176 different territories where falcons were encountered in one or more years. The top two candidate models for the

177 transitional probability of changing states included effects of habitat and linear trends over time (Table 1). A

178 main effects model (Habitat + trend) had 2.1 times more support than a factorial model (Habitat × trend), but

179 both models were equally parsimonious (ΔAICc <1.5). The top two models received 7.2-15.0 times more

180 support than the next best model, which included linear trends in the transition rates (Trend, ΔAICc = 0.042).

181 We used procedures for model averaging in Program Mark to calculate weighted parameter estimates across our

182 set of candidate models, along with unconditional variances that accounted for uncertainty in model selection.

183 *Parameter estimates*. Once a territory was colonized by falcons, the probability of territory persistence remained

184 high and close to unity, both for territories that were occupied by nonbreeders (S_N = 0.958 ± 0.016SE, 95%CI =

185 0.914 to 0.981), or by breeding pairs (S_B = 0.991 ± 0.011, 95%CI = 0.922 to 0.999). The probability of

186 encounter differed by state and was relatively low for territories occupied by nonbreeders (p_N = 0.661 ± 0.034,

187 95%CI = 0.591 to 0.725), but was at unity for breeders (p_B = 1.00). Consistent with the possible effects of direct

188   density-dependence of territory dynamics, the transitional probability that a territory remained occupied by a

189   breeding pair ($\psi_{B\text{-}B}$) was generally higher than the probability of recruitment ($\psi_{N\text{-}B}$), and both parameters

190   exhibited long-term declines over time (Figure 3). The trends in territory dynamics also differed among habitat

191   strata. The coastal habitat was first colonized by falcons, and the transitional probabilities of becoming or

192   remaining a breeding territory were both high ($\psi_{N\text{-}B} > 0.40$, $\psi_{B\text{-}B} > 0.65$) during the first 25 years of monitoring in

193   1976-2000. Falcons colonized new habitats after the turn of the century. In the latter period of our study period

194   from 2001-2017, transitions of territories from nonbreeding to a breeding state were higher in the fjord and

195   inland habitats ($\psi_{N\text{-}B} \approx 0.38$), than the coastal habitat ($\psi_{N\text{-}B} \approx 0.29$). The probability that sites remained active as

196   breeding territories was also high in the fjord habitat ($\psi_{B\text{-}B} \approx 0.67$), intermediate in the coastal habitat ($\psi_{B\text{-}B} \approx$

197   0.46), and lowest in the inland habitat ($\psi_{B\text{-}B} \approx 0.36$).

198   *Population growth*. We adjusted counts of active territories by the state-specific probabilities of encounter,

199   which increased the estimated number of territories occupied by nonbreeders by 51% (C_N/p_N, where $p_N = 0.661$).

200   Due to staggered colonization of the three different habitats, our three time series for population growth of

201   falcons ranged from $T = 11$ years at inland sites to $T = 41$ years for the coastal habitat (Table 2). The annual rate

202   of population change was lowest in the coastal habitat ($\lambda = 1.04$), intermediate at inland sites ($\lambda = 1.11$), and

203   highest in the fjord habitat ($\lambda = 1.23$). Overall, the annual rate of change for peregrine falcons in Norway was a

204   7% increase per year for the $T = 41$ years from 1976-2017 ($\lambda = 1.07$). Based on exponential growth with an

205   annual lambda of 1.07, the predicted doubling time for falcon populations in central Norway is $T_d = 10.2$ years.

206   *Role of contaminants.* A large array of environmental pollutants have been analyzed during our study period, but

207   we report values for the main contaminants that are thought to be important for peregrine survival and

208   reproduction, including DDTs, PCBs (polychlorinated biphenyls) and dieldrin. Our dataset starts in 1976, with

209   two eggs from a failed clutch in south-western Norway. The mean DDT (DDE) levels in a clutch of two addled

210   eggs from 1976 was ca. 20,000 ppb, PCB levels ca. 30,000 ppb and dieldrin levels ca. 1,000 ppb (all wet weight,

211   Nygård 1983, Figure 6). Critical levels for DDE in peregrine eggs have been estimated to be at 3,000 ppb (wet

212   weight), and for dieldrin (HEOD) at 700 ppb (wet weight, Newton 1988). The mean level of DDTs fell below

213   these critical values by the year 2000. Dieldrin has almost disappeared from peregrine eggs in Norway (Figure

214   6). The PCB levels have been, and still are about twice those of DDTs, but the potential consequences of PCBs

215   for negative impacts on bird reproduction remain unclear. Dieldrin levels were high at the start of our study

216   period, but fell quickly after DDT and dieldrin were banned, and have remained low. Eggshell thickness and

217   eggshell indices are still not recovered back to the baseline levels observed during the pre-DDT era (Figure 6). In

218   the case of heavy metals, Newton and Haas (1988) reported a critical level of 3 ppm mercury (dry weight) (or

219   600 ng/g wet weight) in Merlins (*Falco columbarius*), above which productivity was affected. In our study, 6 of

220   42 peregrine eggs (14.2%) had concentrations of mercury above this level up to a maximum level of 880 ng/g

221   (Figure 6). Mercury exposure may affect a small number of breeding pairs but we conclude that mercury has

222   played a relatively minor role for the regional effects on productivity of peregrines in Norway.

223

224   **Discussion**

225 Recovery of peregrine falcons in central Norway has been associated with regional changes in regulation of
226 agricultural chemicals in western Europe after DDT and PCBs were banned for general use. In Norway, DDT
227 and dieldrin were banned in 1970 and PCBs in 1980 (Holt et al. 1979), and dieldrin was banned as a seed-
228 dressing agent in the UK in 1975 (Walker and Newton 1999). Ring recoveries and resightings indicate that
229 peregrine falcons from Norway often spend the winter in the British isles (Bakken et al. 2003). After national
230 bans on the use of organocholorines came into effect, the levels of environmental pollutants in eggs have steadily
231 decreased for peregrine falcons breeding in central Norway. The levels of DDTs and dieldrin are now below the
232 proposed critical levels. Levels of PCBs remain higher, but they are harder to identify and quantify, and would
233 need more thorough examination. PCBs are known to have more subtle effects of reproductive performance,
234 including embryo mortality, edema and deformities (Gilbertson et al. 1991). The lack of eggs available for
235 analyses between 1947-76 is due to the fact that population numbers were extremely low and few pairs of
236 falcons were known to be present or breeders during this period (Haftorn 1971).

237 Exposure to pesticide chemicals, especially DDT and dieldrin were likely the main factor that caused the decline
238 of peregrines in Norway. Studies of the relationship between DDE levels and eggshell thickness in eggs of
239 raptors worldwide have consistently shown a negative relationship (Cade et al. 1971; Enderson and Wrege 1973;
240 Newton and Bogan 1974; Nygård 1983). Thin eggshells will often break during the brooding time (Newton
241 1973), and the clutch will fail. In Norway, the reduction of the shell thickness index in the two eggs mentioned
242 above was on average 23.3% compared to pre-1947 values. The shell thinning after the turn of the millennium
243 seems to be somewhere between 5 and 10%, a level that is believed not to harm reproduction. Whenever the
244 reproductive performance of raptors shows a shell thinning of more than 16-18% over years, population numbers
245 are likely to decline (Newton 1979). The effect of dieldrin is more related to direct mortality of birds (Bogan and
246 Mitchell 1973; Koeman et al. 1969; Newton and Bogan 1978; Reichel et al. 1969). The role of PCBs are
247 debated, but are thought to be a cause of death for long-lived seabirds (Bourne and Bogan 1972; Parslow and
248 Jefferies 1973). In contrast to DDTs, there is no established link between PCBs and eggshell thinning, but PCBs
249 are known to have effects on productivity, teratogenic effects, and other sublethal health effects (Peakall 1975).
250 It seem safe to conclude that the reduced pesticide levels due to the ban on organochlorines such as DDTs and
251 dieldrin, and possible also PCBs, have been of crucial importance for the recovery of Norwegian peregrines .

252 The traditional strongholds for breeding populations of peregrine falcons in Nord-Trøndelag were at coastal
253 sites, but during the period of population recovery, their distribution changed with expansion into new habitats.
254 Starting in 2004-2006, some pairs established themselves in fjord areas, and during the last ten years a further
255 expansion into inland valleys has occurred (Figure 2). We found that the shift in range from the coast to the
256 inland was accompanied by reductions in the transitional probability that a territory was occupied by a breeding
257 pair. Moreover, we also observed a significant decrease in reproductive rate at the coast, to a point where
258 relatively few chicks have been produced there in the last few years, whereas productivity is better in the fjord
259 and inland habitats (Table 3). Therefore, the predicted doubling-time of 10 years for the national population may
260 increase as population growth slows. Rock faces and cliffs along the rugged coastline of Norway provide
261 numerous sites that are suitable for breeding, but scarcity of suitable food resources could be a limiting factor.
262 Long-term declines in the productivity of peregrines at coastal sites may be driven by changes in their food
263 resources (Figure 4). The main classes of suitable prey at coastal sites are small-bodied colonial seabirds such as
264 terns and gulls. The prey-related hypothesis is supported by ongoing declines reported by The Norwegian

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265 Seabird monitoring programme/SEAPOP (http://www.seapop.no/no) (Figure 5). Population numbers of

266 kittiwakes (*Rissa tridactyla)* have seen an almost catastrophic decline on the coast of Central Norway. Negative

267 trends have also been reported for the common gull (*Larus canus*) and terns (*Sterna* spp.), which used to be more

268 common on the coast. Seabirds often were a staple-food for coastal breeding peregrines, but population numbers

269 of prey species have been scarce and erratic during the last decades. On the other hand, the availability of

270 medium-sized prey such as thrushes and corvids in the fjord and inland habitats seems to be more stable and

271 reliable food source (Framstad 2017), and may have contributed to the shift in distribution from coastal to fjord-

272 and inland-breeding peregrines.

273 The pollutant data from peregrine eggs from the Norwegian coast indicate that exposure is now below critical

274 levels. Therefore, there seems to be good support for the food-related hypothesis for explaining the population

275 decline and poor productivity on the coast of central Norway, and also the shift from coast to fjord and inland

276 sites in territory occupancy and reproduction. The underlying causes of changing trophic dynamics in coast

277 habitats are yet to be explained; why are many of the seabird species on the Norwegian coast doing so badly?

278 Ongoing declines could be due to climate change, overfishing, a side of increases in aquaculture production or

279 other large-scale changes in the coastal landscape, or perhaps to natural changes in the North Atlantic ecosystem.

280 Regardless of the underlying cause, our long-term data indicate that ongoing declines in seabird numbers will

281 affect trophic dynamics and impact peregrine falcons as key predator.

282 The occupation-rate in known territories of peregrines in our Nord-Trøndelag study area lies around 70%, and no

283 more than 24 pairs have been known to breed in a single year. A total county estimate of 25-30 breeding pairs

284 suggests a current breeding density of ca. 0.11 to 0.13 pairs per 100 km^2. The Norwegian breeding population of

285 peregrines was estimated to be between 700 and 1,000 pairs in 2013 (Heggøy and Øien 2014), which is

286 comparable to estimates of the historical population in Norway of 500-1,000 pairs before the 1940's (Lindberg et

287 al. 1988). The Norwegian population of peregrine falcons is on a trajectory to full recovery, and approaching a

288 carrying capacity where density-dependence might lead to population regulation. Here, we found that declines in

289 probability of breeding and productivity in coastal habitats were offset by population growth in fjords and inland

290 habitats. Continuing monitoring is needed to determine whether the dynamic distributions are unique to our

291 study population in central Norway or are a general feature among peregrine falcons breeding in Fennoscandia.

292 **Compliance with ethical standards**

293 The authors Nygård, Sandercock, Einvik and Reinsborg declare that they have no conflict of interests. Our

294 article does not contain any studies with human participants or animals performed by any of the authors.

295 Collection of addled eggs for chemical analyses was conducted under permit.

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297 **References**

298 Andreasen NP (1972) Vandrefalk Møn 1972. Fugleværn 4:11-12

299 Bakken V, Runde O, Tjørve E (2003) Norsk ringmerkingsatlas Vol. I. Stavanger Museum, Stavanger, Norway

300   Berger U, Haukås M (2005) Validation of a screening method based on liquid chromatography coupled to high-
301   resolution mass spectrometry for analysis of perfluoroalkylated substances in biota. Journal of
302   Chromatography A 1081 210-217

303   Bogan JA, Mitchell J (1973) Continuing dangers of peregrines from dieldrin. British Birds 66:437-439

304   Bourne WRP, Bogan JA (1972) Polychlorinated biphenyls in North Atlantic seabirds. Mar Pollut Bull 3:171-175

305   Braune BM, Norstrom RJ, Clark TP (17-20 May 1988) Bioaccumulation of PCB congeners, PCDDs, PDCFs
306   and organochlorines in Lake Ontario herring gulls (*Larus argentatus*). 31st Conference on Great Lakes
307   Research. Hamilton (Canada), 1988

308   Cade TJ, Lincer JL, White CM, Roseneau DG, Schwarz LG (1971) DDE residues and eggshell changes in
309   Alaskan falcons and hawks. Science 172:955-957

310   Carson R (1962) Silent Spring. Houghton Mifflin, Boston

311   Enderson JH, Wrege PH (1973) DDE residues and eggshell thickness in prairie falcons. J Wildl Manage 37:476-
312   478

313   Fisk AT, Norstrom RJ, Cymbalisty CD, Muir DCG (1998) Dietary accumulation and depuration of hydrophobic
314   organochlorines: Bioaccumulation parameters and their relationship with the octanol/water partition
315   coefficient. Env Toxicol Chem 17:951-961

316   Fisk AT, Hoekstra PF, Borgå K, Muir DCG (2003) Biomagnification. Mar Pollut Bull 46:522-524

317   Framstad E. (2017) (ed.) Terrestrisk naturovervåking i 2016: Markvegetasjon, epifytter, smågnagere og fugl.
318   Sammenfatning av resultater [In Norwegian]. - NINA Rapport 1376. Norwegian Institute for Nature
319   Research Trondheim. 122 p

320   Frøslie A, Holt G, Norheim G (1986) Mercury and persistent chlorinated hydrocarbons in owls Strigiformes and
321   birds of prey Falconiformes collected in Norway during the period 1965-1983. Environ Pollut Ser B
322   11:91-108

323   Gilbertson M, Kubiak T, Ludwig J, Fox G (1991) Great Lakes embryo mortality, edema, and deformities
324   syndrome (GLEMEDS) in colonial fish eating birds: similarity to chick-edema disease. J Toxicol
325   Environ Health 33:455-520

326   Gjershaug JO, Kålås JA, Nygård T, Herzke D, Folkestad AO (2008) Monitoring of raptors and their
327   contamination levels in Norway. Ambio 37:420-424

328   Haftorn S (1971) Norges fugler. Universitetsforlaget, Oslo

329   Heggøy O, Øien IJ (2014) Conservation status of birds of prey and owls in Norway Vol. 1-2014. Norsk
330   Ornitologisk Forening/Birdlife Norway, Trondheim

331   Helander B, Olsson A, Bignert A, Asplund L, Litzén K (2002) The role of DDE, PCB, coplanar PCB and
332   eggshell parameters for reproduction in the White-tailed Sea Eagle (*Haliaeetus albicilla*) in Sweden.
333   Ambio 31:386-403

334   Hickey JJ (ed) (1969) Peregrine falcon populations, their biology and decline. University of Wisconsin Press,
335   Madison, Milwaukee & London

336   Holt G, Frøslie A, Norheim G (1979) Mercury, DDE, and PCB in the avian fauna in Norway 1965-1976. Acta
337   Vet Scand Suppl 70:1-28

338   Koeman JH, Vink JAJ, de Goeij JJM (1969) Causes of mortality in birds of prey and owls in the Netherlands in
339   the winter of 1968-1969. Ardea 57:67-76

9

340 Lindberg P (1975) Pilgrimsfalken i Sverige. Svenska naturskyddföreningen, Stockholm

341 Lindberg P, Odsjö T (1983) Mercury Levels in feathers of peregrine falcon *Falco peregrinus* compared with total

342   mercury content in some of its prey species in sweden. Environ Pollut 5:297-318

343 Lindberg P, Schei P, Wikman M (1988) The Peregrine Falcon in Fennoscandia. In: Cade TJ, Enderson JH,

344   Thelander CG, White CM (eds). Peregrine Falcon populations. Their management and recovery. pp

345   159-172. The Peregrine Fund, Inc., Boise

346 Linkola P, Suominen T (1969) Population trends in Finnish peregrines. In: Hickey JJ (ed). Peregrine falcon

347   populations. Their biology and decline. pp 183-191. University of Wisconsin Press, Madison,

348   Milwaukee and London

349 Lundholm E (1987) Thinning of eggshells in birds by DDE: Mode of action on the eggshell gland. Comp

350   Biochem Physiol 88C:1-22

351 Murvoll KM, Skaare JU, Anderssen E, Jenssen BM (2006) Exposure and effects of persistent organic pollutants

352   in European shag (*Phalacrocorax aristotelis*) hatchlings from the coast of Norway. Environ Toxicol

353   Chem 25:190-198

354 Newton I (1973) Egg breakage and breeding failure in British merlins. Bird Study 20:241-244

355 Newton I (1979) Population ecology of raptors. T & A.D. Poyser, Berkhamsted

356 Newton I (1988) Determination of critical pollutant levels in wild populations, with examples from

357   organochlorine insecticides in birds of prey. Environ Pollut 55:29-40

358 Newton I, Bogan JA (1974) Organochlorine residues, eggshell thinning and hatching success in British

359   sparrowhawks. Nature, London 249:582-583

360 Newton I, Bogan J (1978) The role of different organochlorine compounds in the breeding of British

361   sparrowhawks. J Appl Ecol 15:105-116

362 Newton I, Haas MB (1988) Pollutants in merlin eggs and their effects on breeding. Brit Birds 81:258-269

363 Nichols JD, Hines JE, Mackenzie DI, Seamans ME, Gutiérrez RJ (2007) Occupancy estimation and modeling

364   with multiple states and state uncertainty. Ecology 88:1395-1400

365 Nisbet ICT (1988) The relative importance of DDE and dieldrin in the decline of peregrine falcon populations.

366   In: Cade TJ, Enderson JH, Thelander CG, White CM (eds). Peregrine falcon populations. Their

367   management and recovery. pp 351-375. The Peregrine Fund, Inc., Boise, Idaho

368 Nygård T (1983) Pesticide residues and shell thinning in eggs of peregrines in Norway. Ornis Scandinavica

369   14:161-166

370 Nygård T (1999) Correcting eggshell indices of raptor eggs for hole size and eccentricity. Ibis 141:85-90

371 Nygård T, Polder A. (2012) Miljøgifter i rovfuglegg i Norge. Tilstand og tidstrender (Pollutants in raptor eggs in

372   Norway. Current state and time-trends.). - NINA Rapport 834. Norwegian Institute for Nature Research,

373   Trondheim. 53 p

374 Parslow JLF, Jefferies DJ (1973) Relationship between organochlorine residues in livers and whole bodies of

375   Guillemots. Environ Pollut 5:87-101

376 Peakall DB (1975) PCB's and their environmental effects. CRC Crit Rev Environ Contr 5:469-508

377 Peakall DB, Miller DS, Kinter WB (1975) Blood calcium levels and the mechanism of DDE-induced eggshell

378   thinning. Environ Pollut 9:289-293

379   Polder A, Venter B, Skaare JU, Bouwman H (2008) Polybrominated diphenyl ethers and HBCD in bird eggs of
380   South Africa. Chemosphere 73:148-154

381   Polder A, Gabrielsen GW, Odland JØ, Savinova TN, Tkachev A, Løken KB, Skaare JU (2008) Spatial and
382   temporal changes of chlorinated pesticides, PCBs, dioxins (PCDDs/PCDFs) and brominated flame
383   retardants in human breast milk from Northern Russia. Sci Total Environ 391:41-54

384   Porter RD, Wiemeywer SN (1969) Dieldrin and DDT: Effects on sparrowhawk eggshells and reproduction.
385   Science 165:199-200

386   Ratcliffe DA (1958) Broken eggs in peregrine eyries. British Birds 51:23-26

387   Ratcliffe DA (1967) Decrease in eggshell weight in certain birds of prey. Nature 215:208-210

388   Ratcliffe DA (1970) Changes attributable to pesticides in egg breaking frequency and eggshell thickness in some
389   British birds. J Appl Ecol 7:67-115

390   Reichel WL, Cromartie E, Lamont TG, Mulhern BM, Prouty RM (1969) Pesticide residues in eagles. Pesticide
391   Monit J 3:142-144

392   Schei PJ (1984) Siste nytt om vandrefalken i Norge. Vår Fuglefauna 7:217-223

393   Walker CH, Newton I (1999) Effects of cyclodiene insecticides on raptors in Britain - correcting and updating of
394   an earlier paper by Walker and Newton, Ecotoxicology 7, 185-189 (1998). Ecotoxicology 8:425-429

395

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Table 1. Model selection for multistrata modeling of territorial occupancy by peregrine falcons in central Norway, 1976-2017. Territories were coded as being unoccupied (0), occupied by nonbreeders (N), or occupied with confirmed evidence of breeding (B). The transitional probabilities of changing states (ψ_{N-B} and ψ_{B-N}) were modeled as linear trends and for three different habitats (coast, fjord, and inland sites), whereas the state-specific estimates of territory persistence (S_N and S_B) and probabilities of encounter (p_N and p_B) were held constant.

Model for probabilities of changing states (ψ)	K	Deviance	AICc	ΔAICc	AICc weights
Habitat + trend	12	810.9	862.9	0.00	0.632
Habitat × trend	16	803.6	864.4	1.45	0.307
Trend	7	826.9	868.3	5.41	0.042
Constant	6	831.3	870.6	7.70	0.013
Habitat	10	824.7	872.4	9.50	0.005

Table 2. Estimates of the finite rate of population change (λ) for peregrine falcons in central Norway, 1976-2017.

Region	Starting year				Ending year				T	λ
	Year	Occ.	Breed	$\hat{N}_1$	Year	Occ.	Breed	$\hat{N}_{T+1}$		
Coast	1976	0	2	2.0	2017	6	1	10.1	41	1.04
Fjord	2004	0	1	1.0	2017	7	4	14.6	13	1.23
Inland	2006	2	0	3.0	2017	3	5	9.5	11	1.11
All	1976	0	2	2.0	2017	16	10	34.1	41	1.07

Table 3. Average reproductive rates of peregrine falcons per occupied territory per decade in three different habitats in central Norway, 1976-2017. Reproductive rates were measured as the number of large chicks recorded at the nest site at the end of the nesting period.

Region	Decade	Mean	SD	N
Coast	1976-79	2.00	1.08	4
	1980-89	1.93	1.07	10
	1990-99	1.58	0.99	10
	2000-09	1.25	0.61	10
	2010-17	0.64	0.39	8
Fjord	2004-09	1.33	0.57	6
	2010-17	1.02	0.39	8
Inland	2006-09	0.96	1.33	3
	2010-17	0.97	0.63	8
Overall	1976-2017	1.31	0.85	67
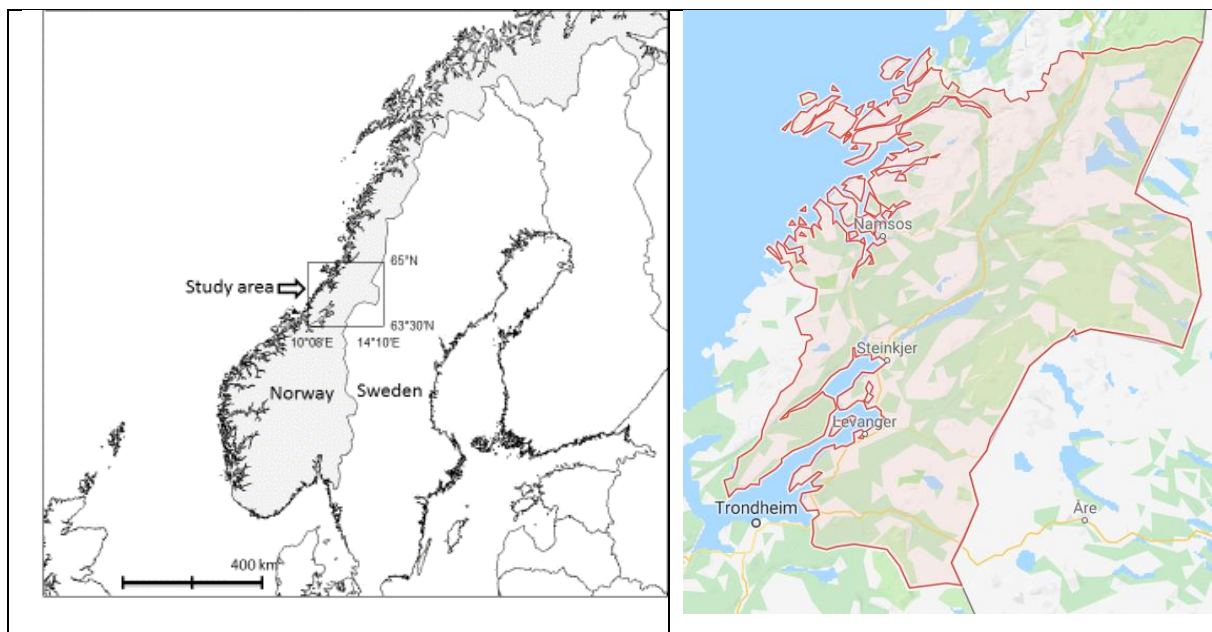
Figure 1.
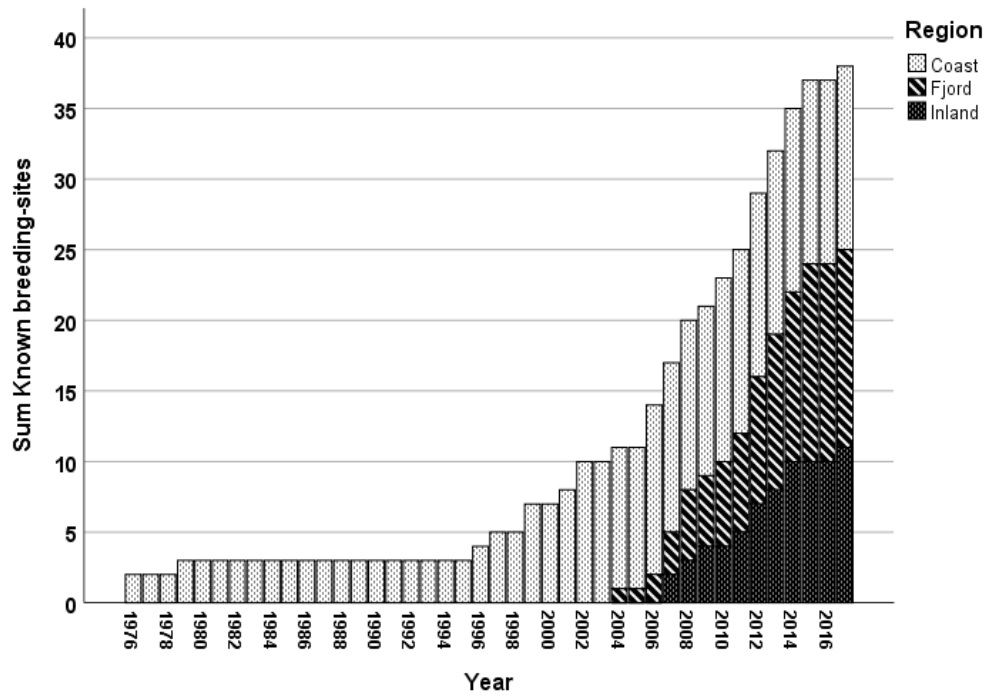
Figure 2.
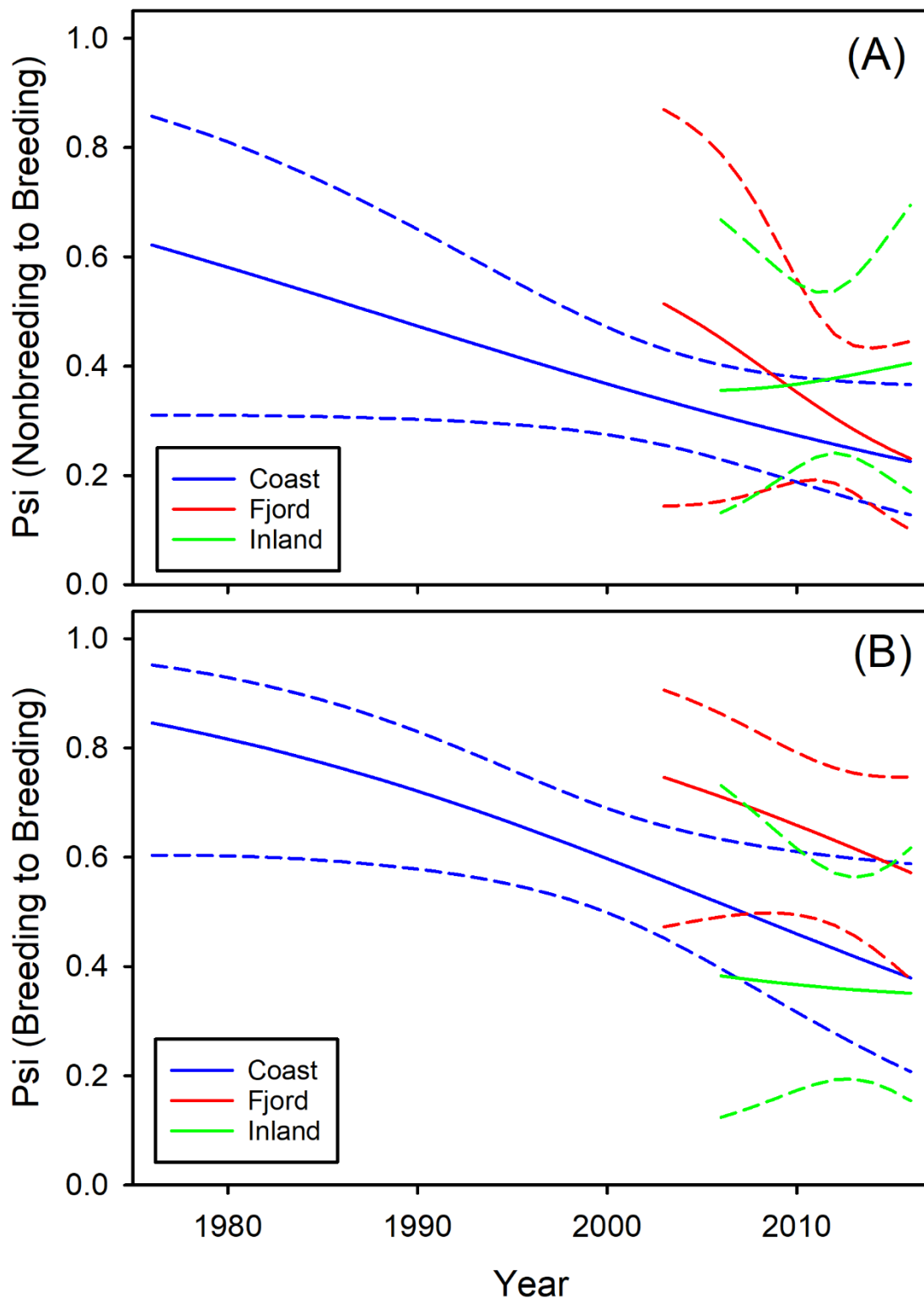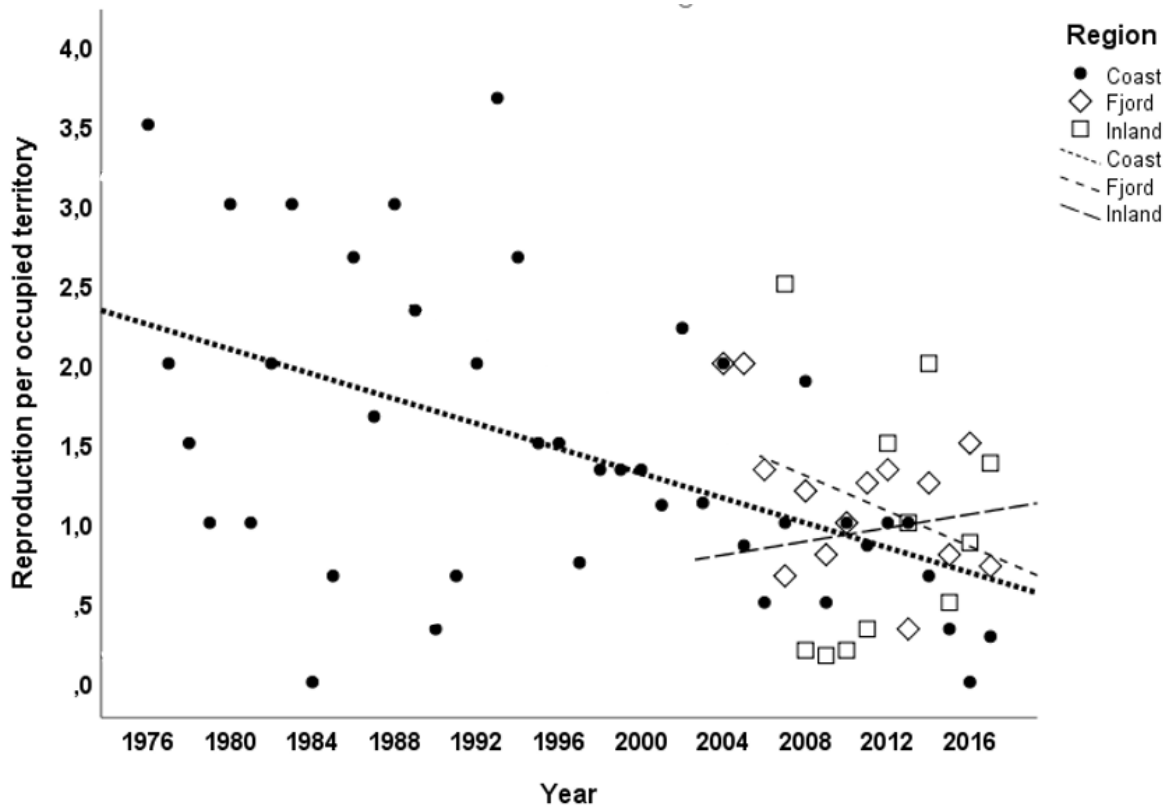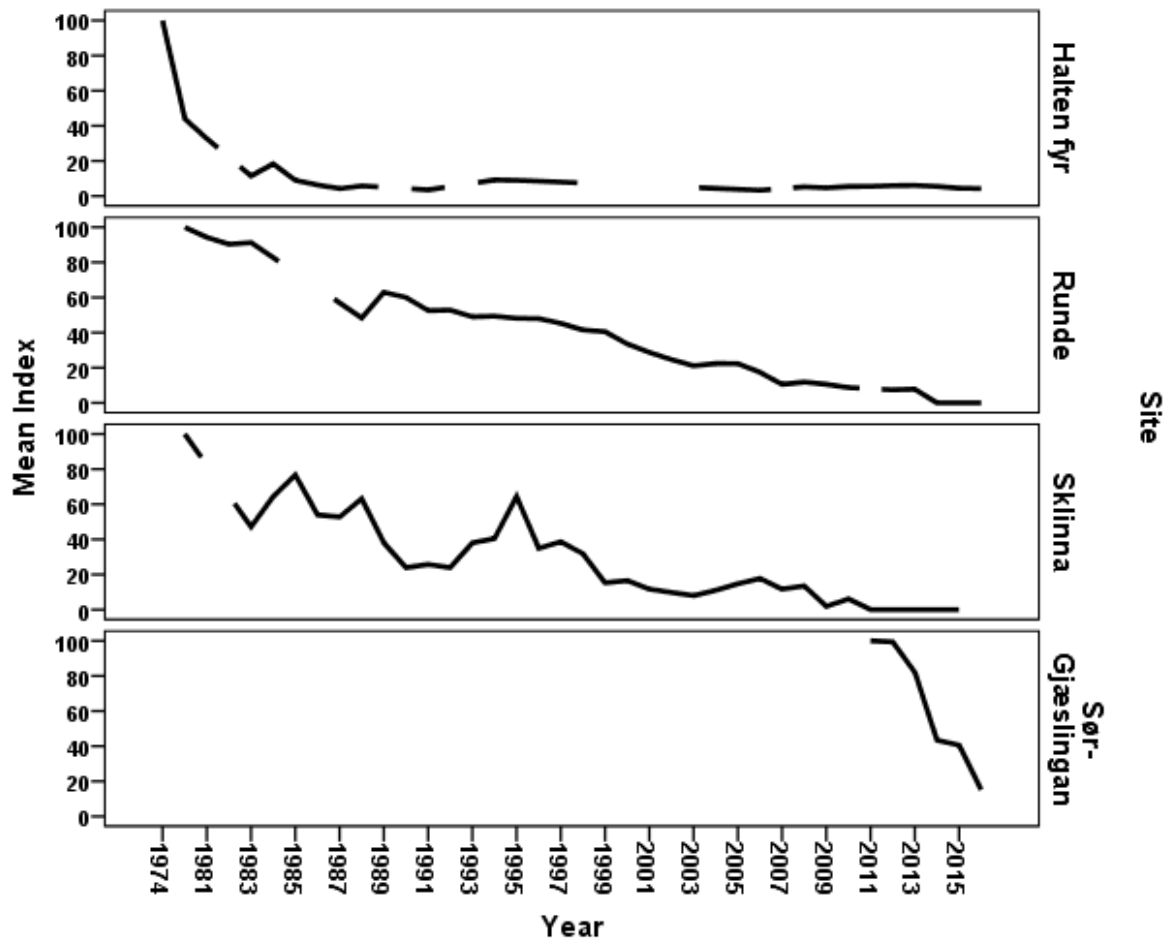
Figure 3.

Figure 4.

Figure 5.

Figure 6.

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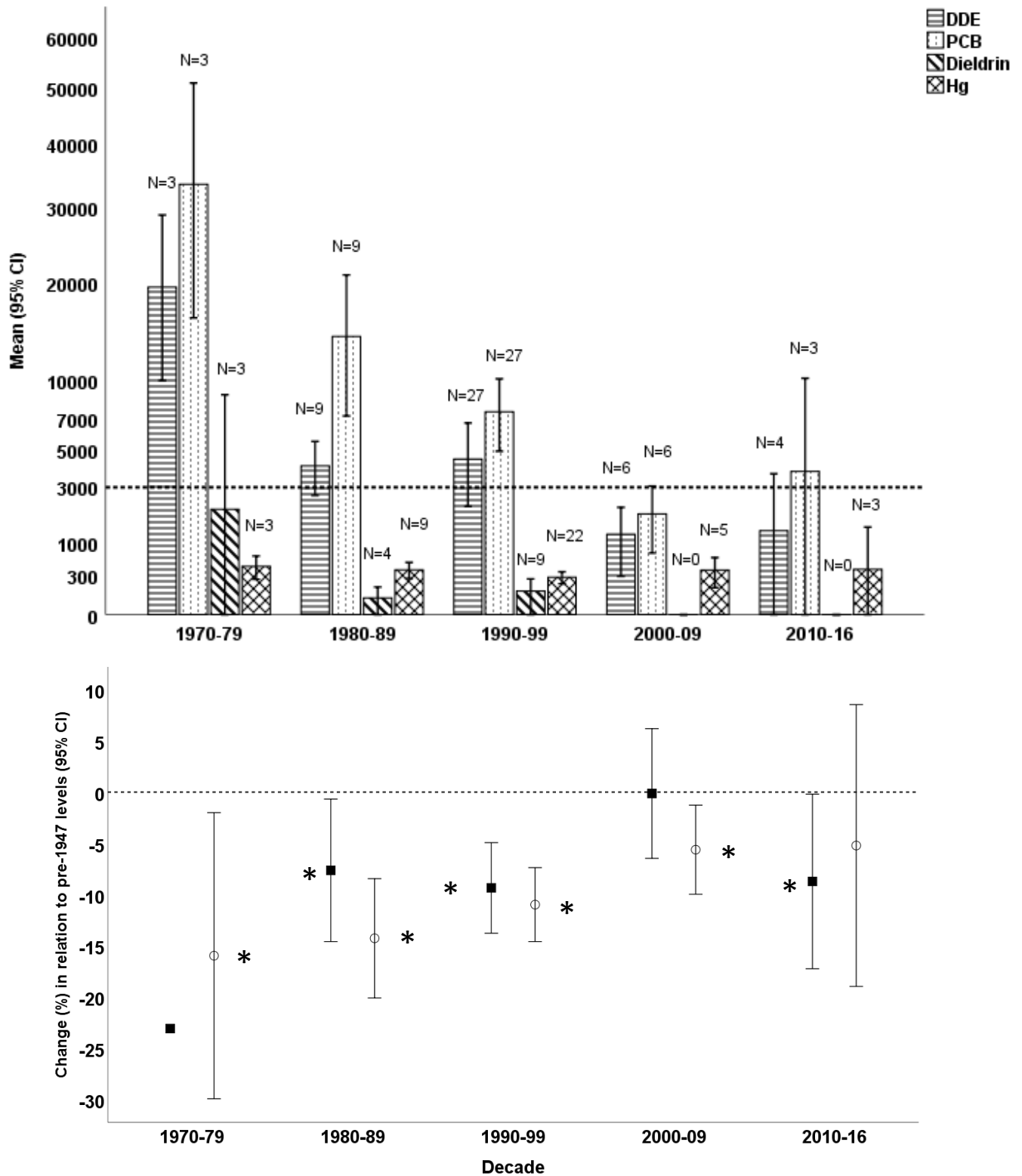**Legend to figures.**

Figure 1. The study area of the former Nord-Trøndelag county (22,412 km^2), Norway.

Figure 2. The cumulative number of known breeding-sites for Peregrine falcons in Nord-Trøndelag county 1976-2017. Not all sites were occupied in any year.

Figure 3. Annual variation in the transitional probability of site becoming or remaining a breeding territory ($\psi \pm$ unconditional 95%CI) for sites occupied by: (A) nonbreeding birds (ψ_{N-B}), or (B) breeding pairs (ψ_{B-B}) of Peregrine Falcons in three different habitats in Nord-Trøndelag county, Norway, 1976-2017.

Figure 4. Reproduction of young per occupied Peregrine territory in Nord-Trøndelag county, Norway 1976-2017, by year and region (habitat), expressed as the number of large chicks late in the breeding season. Coast: R^2 = 0.256, P = 0.001, Y = 79.196 – 0.039 * Year. Fjord and Inland: Not Significant.

Figure 5. Population trends for Black-legged Kittiwakes (*Rissa tridactyla*) at four major colonies in central Norway 1974-2016. The count unit is number of active nests, and the index is the percent remaining relative to numbers in the starting year. Gaps indicate years without surveys. (Source: The Norwegian Seabird monitoring programme/SEAPOP).

Figure 6. Top panel: Mean concentrations of DDE, PCBs dieldrin and mercury (Hg) (on wet weight basis) in eggs of Peregrine falcon in Norway, average per decade, 1976-2017, (95% C.L.). The dashed reference line is the proposed critical level for Peregrine at 3000 ppb DDE in eggs (w.w.), above which, levels are predicted to have a negative population effect (Newton 1988). Bottom panel: Mean reduction in eggshell thickness (squares)(whole eggs and fragments with membranes) and eggshell index (open circles) after 1947 by decade, based on clutch averages. x: P < 0.05, xx: P <0.01, xxx: P < 0.001 (Mann-Whitney U-test), (95% C.L.). The dashed reference line is based on measurements of eggsets from Norway collected before 1947.