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Turnover and post-bottleneck genetic structure in a recovering population of Finnish Peregrine Falcons *Falco peregrinus*

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Dispersal is a process that increases genetic diversity and genetic connectivity of populations. We studied the turnover rate of breeding adults and genetic population structure to estimate dispersal in Finnish Peregrine Falcons. We used relatedness estimates among Finnish Peregrine Falcons over a five-year period, genotyping over 500 nestlings (with 10 microsatellite loci) to reveal the rate of turnover. Our results reveal a high turnover rate (21.65%), which does not seem to be correlated with breeding success of the previous year. The extent of population genetic structure and diversity, and possible signs of the population crash during the 1970's was studied with a reduced dataset, excluding relatives. We found genetic diversity to be similar to previously studied falcon populations (expected heterozygosity of 0.581) and no population genetic structuring among our sampled populations. We did not observe a genetic imprint of the past population bottleneck that the Finnish Peregrine population experienced. We conclude that high dispersal rates have likely contributed to maintaining genetic diversity across the landscape, by mixing individuals within the species' distribution in Finland and thus prevented genetic structuring and negative effects associated with the population decline in the 1970s.

Keywords: raptor dispersal, nest-site fidelity, relatedness, microsatellites, genetic diversity.

Dispersal is a condition-dependent process affecting individual fitness and population dynamics. The occurrence and strength of dispersal can differ over time and even among populations within a species, depending on environmental and social factors (Serrano *et al*. 2001, Morrison & Wood 2009). In animals, dispersal is commonly divided into natal dispersal and breeding dispersal. Natal dispersal is defined as the movement of juveniles to the site of first breeding and breeding dispersal as the movements of mature individuals between consecutive breeding attempts (Greenwood & Harvey 1982, Morrison & Wood 2009). They both have important consequences to population dynamics and evolution in ecological and evolutionary time frames, affecting spacing of individuals, local patterns of age structure, survival and recruitment, persistence of populations and species' distributions (Morrison & Wood 2009).

Dispersal enables the connection of a species' populations across space, the persistence of species despite possible local population extinctions and tracking of suitable habitats in response to changing environmental conditions (Ronce 2007). When spatially distinct populations are connected by gene flow, their genetic diversity often remains greater than if the populations were isolated. In addition to increasing genetic variation, dispersal decreases inbreeding, which is especially important in small populations. Dispersal can rescue populations from extinction: genetic rescue or assisted gene flow has been used on several occasions to increase population sizes and genetic diversity of threatened populations (e.g. Madsen *et al*. 2004, Hedrick & Fredrickson 2010, see Frankham 2015 and Whiteley *et al.* 2015 for reviews).

In most birds, males exhibit greater nest-site fidelity than females. This is observed especially in territorial species, in which the male defends the recourses, and in species with a mating system based on female choice (Greenwood 1980), i.e. female chooses her partner based on for example the quality of a male or of a territory. Thus, females have generally longer natal dispersal distances, they change nest-sites more frequently and move greater distances between nest-sites in different years. In addition to gender, nest-site fidelity is affected by an individual's age, previous breeding success, long-term occupancy and quality of the nest-site and the mate. More specifically, older individuals, successful breeders and individuals inhabiting high quality territories show greater nest-site fidelity (Greenwood 1980, Greenwood & Harvey 1982, Morrison & Wood 2009).

The Peregrine Falcon *Falco peregrinus* is a predominantly nest-site tenacious raptor that inhabits large territories with multiple alternative nest-sites. It is distributed nearly world-wide, absent only from Antarctica. The species generally breeds in precipitous sites, such as cliffs or crags

(Cramp & Simmons 1980). However, in Finland the species (represented by the nominate subspecies *F. p. peregrinus*) primarily breed on the ground in open peatlands, with a few exceptional cliff and tree nesting sites (Below 2000). The territories typically exhibit a neighbour distance of 10 km and hold one to eight alternative nest-sites. After the middle of the last century, the Peregrine Falcon populations declined strongly because of bioaccumulation of organochloride pesticides. This occurred also in Finland between the 1950s and 1970s (Cramp & Simmons 1980, Ollila & Koskimies 2008). Historically, the species' distribution covered the whole of Finland and before the 1940s, its population size was estimated to be around 700–900 pairs (Below 2000, Ollila & Koskimies 2008). At the lowest, only approximately 30 pairs remained at two locations in the northern part of the country. The population started to recover in the 1970s and 1980s (Below 2000) and after that the population growth has been rapid, albeit unsteady between years and areas. Currently, there are around 280-310 breeding pairs (Ollila 2015) and the distribution centers on northern part of the country (Ollila & Koskimies 2008, Fig. 1). The species is classified as vulnerable (VU, International Union for Conservation of Nature [IUCN] classification, Rassi *et al*. 2010) in Finland due to the low population size (criteria D).

Since year 2007, between 150 and 200 Finnish Peregrines have been marked with colour-rings every year. To date, only 56 of them have been re-sighted, most ringed as nestlings. Over half of the re-sightings were from abroad during winter migration (Ollila 2013, Finnish Ringing Centre; query made in June 2016), thus providing little information on the turnover and dispersal in the Finnish population. In the study presented here, we used genetic data to study the dispersal and turnover in Finnish Peregrines. First, we estimated how often breeding pairs are replaced in a territory. Annual turnover in breeding individuals results from mortality and breeding dispersal (nest-site fidelity) and thus provides information on the population structure and dynamics. Turnover was examined using microsatellite genotyping of the offspring and estimating relatedness within and between consecutive nesting attempts within known territories. Second, we estimated the genetic structure and diversity in the Finnish population and tested whether the decline in population size has had any effect on genetic variation.

METHODS

DNA extraction and genotyping

Feather samples were collected from the chicks between 2006-10 during the ringing procedure. All known territories in Finland were visited each year. If breeding was not confirmed at a particular nest-site, the territory was searched for alternate nests. The total sample size (*n*) was 538 and the samples divided into study years as follows: *n* (2006) = 125 chicks, *n* (2007) = 141 chicks, *n* (2008) = 57 chicks, *n* (2009) = 139 chicks and *n* (2010) = 76 chicks. The sampling sites were concentrated in northern Finland, as the species is still rare in the south (Fig. 1). DNA was extracted from feather quills using QuickExtract solution (Epicentre) following the manufacturers' protocol.

We used ten polymorphic microsatellite markers developed for Peregrine Falcons (Nesje *et al*. 2000a) and amplified them in three multiplex PCRs. Multiplex 1 included 0.2 μM of reverse and forward primers for locus NVHfp13, 0.4 μM for locus NVHfp79-4 and 0.3 μM for locus NVHfp89; multiplex 2 included 0.4 μM of both primers for locus NVHfp31 and 0.2 μM for loci NVHfp46-1, NVHfp54 and NVHfp86-2 and; multiplex 3 included 0.4 μM of primers for NVHfp107 and 0.2 μM for loci NVHfp82-2 and NVHfp92-1. The forward primers were labelled with florescent dyes. All multiplexes were performed in 10 μl volumes containing 50–100 ng of template DNA, 0.2 mM of each dNTP, 1 μl of reaction buffer, 2.0 mM $MgCl_2$ and 0.06 units of DNA polymerase (Biotools). The PCR profile was 94°C for five min. followed by 35 cycles of 94°C for 30 s, 55°C for 30 s and 72°C for 45 s and a final extension in 72°C for five min. PCR-amplification reactions were run on a ABI 3730 Genetic Analyzer and alleles were scored with Genemapper v.3.7 (Applied Biosystems).

About 10% of the samples were PCR-amplified twice at all ten loci (Hoffman & Amos 2005) to calculate the genotype error per locus (as it is the most universal metric to use, Pompanon *et al.* 2005). The possible large allele dropouts, scoring errors and presence of null-alleles were searched with the program Microchecker (Van Oosterhout *et al*. 2004) and estimates of null-allele frequencies were calculated with the program ML-Relate (Kalinowski *et al*. 2006) using the maximum likelihood method by Kalinowski and Taper (2006).

Relatedness and substitution of parents

To assess the feasibility of the set of loci used for relatedness analyses, we estimated the cumulative probability of identity (P_{ID}) and probability of identity of siblings ($P_{ID(sib)}$) with the program Gimlet v.1.3.3. (Valière 2002), and searched for identical genotypes using the Microsoft Excel macro Genecap (Wilberg & Dreher 2004), within a dataset from 530 individuals (eight individuals were

excluded due to extensive missing data). To be able to detect substitution of a parent or both parents, we calculated relatedness-values between siblings within a nest and between subsequent nests within the same territory. These data consisted of 365 chicks from 71 territories with two to four successive nestings, altogether 168 nestings (average 2.4 nestings per territory). In 50 territories, two successful (= at least one chick produced) nestings were observed. In 15 territories there were three successful nestings and in six territories four successful nestings. Difference in yearly numbers of nests and chicks at the time of ringing was tested with the χ^2-test. We included all successful nests in the analyses, even when there were intervening breeding seasons with no breeding or unsuccessful nesting (= no chicks produced). We also took into account the total number of chicks even if they were not all sampled for DNA (this led to a total number of 567 chicks, 242 nests and 149 territories, Table 1).

The relatedness-values were calculated using the maximum likelihood estimate of relatedness, which accounts for null-alleles (*r*; Wagner *et al*. 2006), implemented in the program ML-Relate. The difference in relatedness of within and between nests was tested with the Mann–Whitney *U*-test. To identify the nests, where one or both parents had turned over between years, we examined the difference in relatedness values between subsequent nestings within a territory. We used as a cutoff-value of a minimum of 40% drop of relatedness between nests from the mean within-nest relatedness. We chose not to use the exact decrease by 50% that would be expected if one of the parents had changed to allow some variance. A drop of 40% is large enough to likely avoid a chance result. This criterion led to an average cutoff-value of 0.297 for relatedness between subsequent nests. It is possible that a drop in relatedness is also due to complete turnover of a pair at a given territory, therefore we used a lower limit for the relatedness-values and set a 85% decrease as a maximum (average lower limit was relatedness of 0.074). We used the χ^2–test to detect temporal variation in the amount of territories where adult(s) had turned over.

Genetic diversity and population structure

We resampled one nestling per territory to avoid sampling relatives and formed one dataset covering all the years (n = 145) for population genetic analyses. Since the turnover estimates were calculated on yearly datasets, we also estimated the genetic diversity for each year separately with

resampling one nestling per territory. The yearly sample sizes (*n*) were as follows: 2006 (57), 2007 (68), 2008 (27), 2009 (58) and 2010 (33).

The observed (H_O) and expected heterozygosities (H_E), numbers of alleles, allelic richness and deviations from the Hardy-Weinberg equilibrium were estimated using the program FSTAT v. 2.9.3. (Goudet 2001) and linkage equilibrium was tested using the program Genepop v. 4.1. (Raymond & Rousset 1995). The effective population size (N_e) was estimated with the program ONeSAMP v. 1.2 (Tallmon *et al*. 2008) that uses approximate Bayesian computation. We used an *a priori* distribution of 30 to 500 pairs, with the lower bound based on the number of known pairs during the bottleneck and the upper bound based on the approximate number of current breeding pairs in Finland. The estimates of N_e were calculated for the combined data over the study years and for each year separately. In addition, we ran the program with four additional *a priori* distributions to assess the estimate's sensitivity to the choice of the distribution. In order to further evaluate the robustness of estimated N_e values, we derived estimates of N_e using the program NeEstimator v.2.01 (Do *et al.* 2013), using the linkage disequilibrium method, assuming monogamy and the values of 0.05, 0.02 and 0.01 for the lowest allele frequencies.

We used the program Structure v. 2.3.1 (Pritchard *et al*. 2000) to investigate population genetic structure. The program uses a Markov chain Monte Carlo (MCMC) approach to identify the number of genetically distinct clusters (*K*) in a dataset without prior information of the sampling locations. We used the admixture model with correlated allele frequencies and ran the program for 100 000 MCMC replicates with a burnin of 10 000 for ten iterations with *K* set from one to five. We calculated the likelihood of the data for each value of *K*. Structure was run only with the combined dataset across years (n = 145).

To determine if isolation-by-distance among our sampled populations was a likely contributing factor to observed levels of population structure we made use of the program SpaGeDi v.1.3. (Hardy & Vekemans 2002). We calculated the regression between kinship coefficients (Loiselle *et al*. 1995) between pairs of individuals and their respective geographic distances on a logarithmic scale. We used the spatial coordinates of the nest-sites and the equal frequency method to create ten distance classes (Escudero *et al*. 2003). Individual spatial locations were randomized across 10 000 iterations to test for spatial structure and standard errors for each distance class were obtained by jackknifing over loci (Hardy & Vekemans 2002). In SpaGeDi, we used only the combined across years data (n = 145).

Demographic history was assessed by testing for a bottleneck using the program Bottleneck v. 1.2.02 (Cornuet & Luikart 1996). All mutation models, IAM, SMM and TPM (variance set to 70% of SMM) were used and tested with the Wilcoxon sign rank test along with the mode shift test. In addition, we calculated the Garza-Williamson index (Garza & Williamson 2001) with Arlequin v. 3.5.1.3. (Excoffier *et al*. 2005). Demographic history was assessed based on the combined across year data (*n* = 145).

RESULTS

Data quality was high with 94% PCR-amplification success and the genotyping error rate was low: the error rate varied between 0 and 0.073 among loci, which yielded an average error rate of 0.019 over all loci (Table 2). The presence of null alleles was detected at three loci (NVHfp79-4, NVHfp92-1, NVHfp82-2) in the dataset with all years pooled, with a frequency of 0.0485 at locus NVHfp79-4, 0.0938 at locus NVHfp92-1 and 0.0115 at locus NVHfp82-2. However, this was not consistent when the data for each year was tested individually (2006 and 2010: no indication of null-alleles; 2007: possible null alleles at NVHfp82-2, 2008: possible null-alleles at NVHfp46-1 and NVHfp79-4, 2009: possible null-alleles at NVHfp79-4). Previous studies on Peregrine Falcons, using the above mentioned loci have occasionally detected null alleles (e.g. Nesje *et al.* 2000a, Brown *et al*. 2007, Jacobsen *et al*. 2008, Johnson *et al*. 2010), and attributed this result most often to Wahlund's effect, i.e. excess of homozygosity due to population genetic structures. Based on the inconsistent results across different years, we assumed that the observation of null alleles was a statistical artifact and included all loci in the analyses below. There was no evidence of large allelic dropout or scoring errors.

Relatedness and substitution of parents

The cumulative probability of identity for siblings was 0.00137 and the cumulative probability of identity was $6.680 * 10^{-8}$ (all ten loci used). There were two genotypes shared by two individuals. The first was shared between two siblings from the same nest (in this territory there was only one nesting attempt during the follow-up period) and the second by two chicks from different territories (the other one from a territory with only one nesting attempt and the other from a territory with

successive nesting attempts across the study years). These results suggest that the loci used were of sufficient power for meaningful estimates of relatedness to be derived in our study.

The numbers of chicks and nests per year varied significantly (χ^2 = 33.41, *df* = 4, *P* < 0.001 for chick numbers and χ^2 = 13.12, *df* = 4, *P* < 0.05 for nest numbers). The year 2008 had an especially low numbers of chicks (*n* = 59) and nests (*n* = 29) while for 2007 very high numbers of chicks (*n* = 148) and nests (*n* = 70, Table 1) were discovered. Relatedness between siblings across the study years varied from 0.0878 to 0.806, the mean being 0.495 (*SD* = 0.131); in three cases the relatedness within a nest was below 0.3 and in three cases above 0.7. Relatedness between chicks from different nests within a territory varied from 0 to 0.762 (mean = 0.376, *SD* = 0.178), with 23 cases below 0.3 and two above 0.7. The difference in relatedness within nests and between nests within a territory was significant (Mann–Whitney *U*-test = 1354, *P* < 0.01; Fig. 2).

We observed an indication of adult(s) turnover in 21 territories. They showed a 40% drop in relatedness between nests within a territory as compared to mean within-nest relatedness (mean within-nest relatedness of these nests was 0.551, *SD* = 0.137, the mean relatedness between nests below the cutoff-value (40%) was 0.158, *SD* = 0.105). Altogether, 13 cases were from territories with two successful nests, three with three successful nests and five with four successful nests. In ten cases the territory did not produce any chicks the year preceding (hereafter a year of no nesting) the assumed turnover event. When there were chicks in the preceding year (*n* = 11), the number of chicks varied from one to four. In six cases, the relatedness-value was below the lower limit of 85% of within-nest relatedness. The difference between nests within a territory and nests below the cutoff-value was significant (Mann–Whitney *U*-test = 236.5, *P* < 0.01; Fig. 2). Four of the changes occurred between 2006-07, three between 2007–08, six between 2008–09 and eight between 2009–10 (Table 3).

From all the possible turnover events (*n* = 97), 76 cases showed no turnover of adult(s) in the territories. Twenty-five turnover events preceded a year of no nesting and 51 a year of successful nesting. From the 21 turnovers of adult(s) on territories, 10 occurred after a year of no nesting and 11 after a year of successful nesting (χ^2 = 0.97, *df* = 1, *P* = 0.323). The turnover rate was 14.09% when estimated from the number of territories (*n* = 149) and 21.65% when estimated from the possible turnover events between consecutive nestings (*n* = 97), including turnover of one or both parents. Annually, a replacement occurred in 5.7% of the occupied territories between 2006–07, 10.3% between 2007–08, 10.9% between 2008–09 and 25% between 2009–10.

Genetic diversity and population structure

The expected heterozygosity varied from 0.385 to 0.887 among the loci and the mean H_E over the loci for the pooled data was 0.581. The number of alleles and allelic richness varied between two and 12, the means being 5.60 and 5.59, respectively. Three loci, the same loci that contained putative null-alleles, showed a significant excess of homozygotes from the Hardy-Weinberg expectations (Table 2). One pair of loci was in linkage-disequilibrium after Bonferroni correction (NVHfp79-4 and NVHfp82-2, $P < 0.0011$). However, as previous studies on Peregrine Falcons have not detected linkage between these loci (e.g. Brown *et al*. 2007, Jacobsen *et al*. 2008, Johnson *et al*. 2010), we assumed that this was a statistical artifact of conducting multiple comparisons and both loci were retained in subsequent analyses. The estimates of genetic diversity were very similar among the years (Table 4), except that the yearly samples were mostly not in HW-equilibrium (Table 4), due to the same three loci that were suspect for null alleles. The lowest diversity values (except for expected heterozygosity) were from 2008, when the number of nests and chicks was the lowest. No linkage-disequilibrium was observed in the yearly datasets. The estimate of N_e for the pooled data was 203 (*95% CL* 164.2–296.4) when calculated with the program ONeSAMP. The estimates with alternative *a priori* distributions didn't differ significantly from this value. The yearly estimates were low, varying between 31 and 83 (Table 4). The estimate of N_e from the program NeEstimator was 498 (*95 % CI* 275–1524, with the lowest allele frequency of 0.05). The decrease of the lowest allele frequency used increased the N_e to 628 (*95% CI* 348–2043). Yearly estimates from NeEstimator varied from 429 to infinite, with huge confidence intervals, suggesting that the sample sizes for a reliable yearly estimate of N_e were not large enough to enable meaningful estimation.

The most likely number of populations (*K)* given the data inferred with the program Structure was one (mean *LnP*(1) = -3351.39, mean *LnP*(2) = -3545.01 and decreases further for larger values of *K*). The large difference in likelihood between $K = 1$ and $K = 2$ and the fact that individuals were inferred to belong to both inferred cluster with almost equal probabilities when *K* was set to two, suggest that there is no subdivision in the population.

There was no isolation-by-distance effect in the population ($r^2 = 0.00007$, $P > 0.17$ for negative and $P > 0.82$ for positive slopes). The mean relatedness of the ten distance classes varied randomly

from positive to negative, only one class was significantly different from zero (class 4, mean distance 121 km, mean relatedness 0.008, $P < 0.01$).

The Bottleneck tests were all non-significant after Bonferroni correction. The distribution of allele frequency classes followed the expected L-shaped distribution. The Garza-Williamson index was 1.00. The results were the same for the separate years and for the pooled dataset.

DISCUSSION

Turnover rate

We recovered a high turnover rate (21.65%) of breeding adults in the 71 occupied territories where at least two broods where genotyped over the five study years. Across all 149 territories, the turnover rate was 14%, however, since this result includes territories for which only a single brood was genotyped, we view the higher estimate as more indicative of the population. Annually, from three to eight replacements of parent(s) were observed. Very similar turnover rates have been found elsewhere. In a Canadian population of breeding Peregrines, the turnover rate was 22.00% (15.00% for males and 26.00% for the females, Court *et al.* 1989). Since the males were not observed to move between territories, the male turnover was assumed to result only from mortality. In contrast, females were observed to move between territories, thus turnover of the female portion of the population resulted from both mortality and breeding dispersal (Court *et al*. 1989). In a seven-year study in Scotland, the annual turnover for both sexes together was estimated to be almost as high as our estimate, 19%. The observed turnover was suggested to result from both mortality (maximum mortality 11%) and breeding dispersal (8%, Mearns & Newton 1984). Other estimates of nest-site fidelity in Peregrines are more variable depending on the study population and methods used. In the midwestern United States, out of 241 nestings, only ten adults (4.1%) switched territories (Tordoff & Redig 1997). In a Russian population, very low nest-site fidelity was observed (67%) relative other Peregrine populations as only six out the nine females followed with satellite transmitters returned to the previous years breeding territory (i.e. 33% switched; Sokolov *et al*. 2014).

Our method of genotyping nestlings with microsatellites and calculating relatedness within nests and between nests within the territories, proved to be powerful. Only one other study has applied this method to study the turnover in Peregrines. Nesje *et al*. (2000a) used data from

nestlings of six nest-sites over a period of three years in southern Norway. They found that using a relatedness cut-off value of 0.35 excluded the possibility that nestlings were unrelated with more than 95% confidence. We scaled our cut-off values by the estimated within-nest relatedness, which led to a lower average cut-off value than used by Nesje *et al*. (2000a). This might have biased the turnover rate towards false negatives. Nesje *et al.* (2000a) observed much higher nest-site fidelity compared to our result: out of the 18 possible replacements, only one was detected (5.6% turnover).

With our data, it is not possible to distinguish between mortality and dispersal as the cause of adult turnover. Most likely it results from both. Based on a recent review, the annual survival of Peregrine Falcons varies between 0.701 and 0.859, thus giving a rather low rate for annual adult mortality (0.141–0.290), which is a typical life-history trait to many raptors (Newton *et al*. 2016). It is known that the growth rate of raptor populations is proportionally more dependent on adult survival than the reproductive rate (Stahl & Oli 2006, Wootton & Bell 2014). Since the number of breeding pairs in Finland has grown almost 10-fold during the last 30 years (Ollila & Koskimies 2008) and is still growing, it could suggest that adult mortality has a smaller role in the observed territorial turnover.

Breeding dispersal is the other factor behind adult turnover and it has been observed in this species previously, especially for females (e.g. Zuberogoitia *et al*. 2009). Breeding dispersal can be affected by previous breeding success (e.g. Haas 1998, Hoover 2003, Pakanen *et al*. 2011) among other factors (e.g. age of the dispersing individual and quality of the nest-site and the mate, Greenwood & Harvey 1982). However, we found that over half (11) of the territories that experienced the turnover of an adult(s) had produced chicks in the previous year. This has been documented in other falcon species (*F. columbarius*; Warkentin *et al*. 1991, *F. mexicanus*; Lehman *et al*. 2000, *F. rusticolus*; Booms *et al*. 2011), but not for all raptors (e.g. *Accipiter nisus*, Newton & Wyllie 1992). Assuming that mortality is not the major explanatory factor underlying the observed turnover, it appears that success during the preceding breeding may not unduly influence breeding dispersal in the Finnish Peregrine population. More data on individual fates (re-sightings of colour banded birds and/or satellite tracked birds) are required to test this hypothesis.

A recent study of another falcon species in Finland, the Common Kestrel *Falco tinnunculus*, found that individual strategies during breeding dispersal were influenced by a combination of individual traits (e.g. sex and body condition) and ecological factors (e.g. prey abundance, Terraube

et al. 2015). This could be the case in the Finnish Peregrine Falcon. Of the ecological factors, for example, spring weather conditions could be affecting the nest-site fidelity as the nests located on the ground are prone destruction from heavy rain and other extreme weather conditions (Ranta & Halkka 2008, Ollila 2013). The Finnish Peregrine population has been monitored from the 1970s onwards and when that long-term data was summarized, it was shown that constant occupancy of a territory (3 or more years in a row) is quite rare in our study population (Ranta & Halkka 2008). Instead of mortality, such a trend is more likely to result from breeding dispersal as the individuals' could be changing territories due to fluctuating environmental conditions. Thus, environmental conditions could be a proximate driver of breeding dispersal in the Finnish Peregrine population

Genetic diversity, population structure and dispersal

Genetic diversity of the Finnish Peregrine Falcon population (H_E: 0.581, *AR*: 5.59) is similar to that of Peregrine Falcon populations in Europe (e.g. in Scandinavia and Scotland H_E: 0.453–0.508; Nesje *et al*. 2000b, in southern Scandinavia H_E: 0.500 and *AR*: 4.06; Jacobsen *et al*. 2008, in Czech Republic H_E: 0.632 and *AR*: 5.83; Bryndová *et al*. 2012) as well as in North America (e.g. *AR*: 3.79–4.59; Brown *et al*. 2007, H_E: 0.485–0.557 and *AR*: 3.70–4.60; Johnson *et al*. 2010). In Australia, the genetic diversity seems to be somewhat lower (H_E: 0.447 and *AR*: 2.06) and even a monomorphic population has been found from the island of Fiji (Talbot *et al*. 2011). Genetic diversity values similar to those from European and North American Peregrine populations have been observed also in other falcons, for example, in the American Kestrel *Falco sparverinus* (H_E: 0.475–0.525, *AR*: 3.31–3.97; Miller *et al.* 2012), but also lower (e.g. island populations of the Common Kestrel, H_E: 0.250–0.480, *AR*: 1.25–1.50; Hille *et al*. 2003) and higher (e.g. Saker Falcon *Falco cherrug*: H_E: 0.649–0.788 and Lanner Falcon *Falco biarmicus*: H_E: 0.653–0.833; Nittinger *et al.* 2007) estimates have been found, using at least partly overlapping microsatellite loci. In many of the above mentioned Peregrine populations, reintroductions have been performed after the decline. In southern Scandinavia, offspring of captive birds originating from Fennoscandia and Scotland were introduced, resulting in introgression from these captive stocks to the remaining native population (Jacobsen *et al*. 2008). Extensive reintroductions were also performed in North America, with thousands of individuals released from either subspecies specific (Canada) or mixed (United States) captive stocks (Tordoff & Redig 2001, Brown *et al*. 2007). Comparisons between contemporary and historical (pre-

bottleneck) Peregrine populations have shown that the genetic diversity has not decreased due to the population decline (Brown *et al.* 2007). Further, the level of genetic variability has been shown to be at the same level between bottlenecked and non-bottlenecked Peregrine populations (Nesje *et al*. 2000b). Our diversity estimates of the Finnish population fell within these values thus, it seems likely that the bottleneck did not substantially decrease the genetic variation of the Finnish Peregrine Falcon population.

The estimated effective population sizes (ONeSAMP: 203, NeEstimator: 498) are below the critical level of N_e 500 (or the recently proposed 1000; Frankham *et al.* 2014) that is needed in the long-term for a population to retain its genetic viability in the form of evolutionary potential (Franklin 1980, Jamieson & Allendorf 2012). The yearly estimates were much below this estimate (ONeSAMP: 21–83), most likely due to the smaller sample sizes. If the population continues to grow in the future, the effective size will increase and hopefully approach the critical level, but genetic monitoring is needed to be able to follow the progress in N_e.

We found no genetic structuring in the Finnish Peregrine Falcon population and no support for isolation-by-distance among sampled localities. The species was restricted to two separate geographic areas in the northern Finland during the population crash in the 1970s, but started to grow without any reintroductions after the banning of organochlorine pesticides. Currently the species is mostly continuously distributed and seems to have reached panmixia (i.e. random dispersal). Indeed, after the bottleneck, there were plenty of free good-quality habitats available so there were no limits to the dispersal. Peregrine Falcon subspecies seem to have generally low genetic structure (Brown *et al*. 2007, Johnson *et al*. 2010) and the low divergence extends to some comparisons between subspecies as well. For a species that can disperse well, low genetic structuring is expected, although it has been demonstrated differentiation can evolve between geographically distant populations, especially if a barrier to dispersal is present across the landscape. For example in Fennoscandia, populations from the southern Scandinavia and northern Fennoscandia (within *F. p. peregrinus*) are genetically differentiated with microsatellite F_{ST}-values ranging from 0.058 to 0.110 (Nesje *et al*. 2000b, Jacobsen *et al*. 2008).

We could not detect any genetic effects of the past population bottlenecks, even though the historical bottleneck is well documented. Similar result has been observed in the North American and southern Scandinavian populations of the Peregrine Falcon that also experienced bottlenecks. (Brown *et al.* 2007, Jacobsen *et al*. 2008). It has been argued that a failure to detect bottlenecks,

even though they have existed, can be due to long generation times that buffer against the genetic erosion caused by the bottlenecks (Hailer *et al*. 2006). Peregrine Falcons do have a relatively long lifespan with a generation length of 6.8 years (Birdlife International 2016) and a maximum lifespan around 17 years (Tordoff & Redig 1997).

Another explanation for the failure to detect bottlenecks can be inter-population movements of birds (both natal and breeding dispersal), which may counteract loss of genetic diversity (Brown *et al*. 2007). In addition to the panmixia within the Finnish population, immigration from populations further away may have contributed to the retention of genetic diversity. There are a few observations from ringed breeding individuals that confirm gene flow between the Finnish and Swedish (Norrbotten) Peregrine populations (Ranta & Halkka 2008).

Earlier studies have shown that in Peregrines, natal dispersal distances are greater than breeding dispersal distances (Mearns & Newton 1984). The mean natal dispersal of the species is estimated to be around 80–220 km for females and 60–110 km for males, with distances over 3000 km recorded (Mearns & Newton 1984, Zuberogoitia *et al.* 2008, Dennhardt & Wakamiya 2013, Faccio *et al.* 2013). Information on breeding dispersal distances is scarce, but distances of 12–90 km for females have been reported from Russia (three females dispersed out of nine birds followed; Sokolov *et al*. 2014) and 29 km in Scotland (Newton 1979). Thus, the lack of genetic structuring in the Finnish population may be more due to natal dispersal than breeding dispersal. As we did not observe any trend of isolation-by-distance, the individuals do not generally have any tendency to return to breed close to the birth place (i.e. philopatric behaviour). To date, recoveries from Finnish colour-ringed birds indicate that natal dispersal distances vary between 11 and 231 km (mean 126 km, n = 14). Observations of breeding dispersal based on colour-ringed birds are still scarce, only two birds were re-sighted and they were both seen (five years later and one year later) in the same territory where they were ringed. Since the nest-sites are difficult to access and most of them are visited only once during the breeding season, the number of observations is quite small. Although we demonstrate that significant breeding turnover occurs in our Finnish population of Peregrines, more data on the movement of individual birds are required to untangle the underlying drivers of dispersal.

Conclusions

Dispersal in Finnish Peregrine Falcons plays a large role in the formation of the present population genetic structure. Since the population crash of the 1970's mixing of individuals, especially trough natal dispersal, may have counteracted the negative effects of the population bottleneck. Thus, the Finnish population has survived the bottleneck without reintroductions and is still growing, in 2015 there were already 136 territories producing offspring (Ollila 2015). Despite the recent growth, the effective population size is still too small for genetic viability in the long-term and thus, genetic monitoring is needed. The observed turnover rate of 21.65% is comparable to many previously studied populations. If low adult mortality is assumed the observed high turnover rate of the breeding birds may occur independent of previous breeding success.

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Table 1. Total numbers of chicks, nests and territories detected across 2006–2010 (counts include chicks that were not sampled for genetic analyses and nests that were not taken into account in the turnover analysis, see text for details). Several same territories were occupied across different study years.

	Year					
	2006	2007	2008	2009	2010	Total
Chicks	147	148	59	133	80	567
Nests	56	70	29	55	32	242
Territories	56	70	29	55	32	149

Table 2. Expected (H_E) and observed (H_O) heterozygosities, number of alleles (A), allelic richness (AR), inbreeding coefficients (F_{IS}) and error rates (ER) from each of the studied loci with the number of successfully PCR-amplified individuals for each locus in the resampled data set over the study period (n). Standard deviations are shown in parenthesis and significant deviations ($P < 0.05$) from Hardy-Weinberg equilibrium expectations in bold. The second reported mean (seven loci) is the average without the three loci that include putative null-alleles. Effective population size (N_e) with the 95% confidence interval in parenthesis is estimated over all study years.

Locus	n	H_O	H_E	A	AR	F_{IS}	ER	N_e
fp13	145	0.6552	0.6815	6	6	0.039	0.035	N/A
fp31	145	0.6345	0.6472	5	4.99	0.020	0.000	N/A
fp46-1	145	0.4207	0.4512	2	2	0.068	0.000	N/A
fp54	145	0.4897	0.4653	6	5.97	-0.053	0.000	N/A
fp79-4	144	0.7986	0.8874	12	12	0.100	0.073	N/A
fp82-2	145	0.2690	0.3244	6	5.99	0.171	0.034	N/A
fp86-2	145	0.6345	0.5780	3	3	-0.098	0.000	N/A
fp89	143	0.7343	0.7796	7	7	0.058	0.018	N/A
fp92-1	144	0.4722	0.6065	6	6	0.222	0.017	N/A
fp107	144	0.3819	0.3849	3	3	0.008	0.017	N/A
Mean		0.5491	0.5806	5.60	5.59	0.055	0.019	203
		(0.1682)	(0.1773)	(2.80)	(2.80)	(0.086)	(0.023)	(164-296)
Mean		0.5644	0.5697	4.60	4.59	0.006		
(seven loci)		(0.1332)	(0.1424)	(1.9)	(1.90)	(0.061)		

Table 3. Yearly numbers of chicks sampled for DNA in the territories of subsequent nests together with information of turnover of adults given as different shading. Light grey = no adult turnover, dark grey = turnover of one parent, black = turnover of a breeding pair, # chicks = total number of chicks per year, # nests = total number of nests per year.

	Year				
Territory	2006	2007	2008	2009	2010
1		3		4	2
2	3			2	
3		2		3	
4	2	2		1	
5		3		3	
6		3		1	
7	2		4		
8				3	2
9	4	4		3	2
10		1		3	
11	1				3
12	2				4
13	4	2		3	4
14	1			4	
15			3	2	
16		2		2	
17		1			3
18		2	2		
19	2		1		
20				2	2
21	2	2			
22		1	2	1	
23	3		1	1	4
24		2			3
25	2	3			
26	3	4	3		
27	3	4			
28	2		1		
29	1	1			
30	1	1			3
31		1			1
32	1	1			
33			2	1	
34		3	1	1	
35	2	1		2	
36	1	1			
37	1			1	

	Year				
Territory	2006	2007	2008	2009	2010
38		1			1
39	3	3			
40	2	3			
41	4	1			
42	3	1			
43		2	3	1	2
44				3	3
45		1		3	1
46			3	2	2
47				2	2
48			1		2
49		3		2	
50		1		2	
51		3	2		
52	3	2	2	4	
53			1	3	
54			1	3	
55			1	3	3
56		1			2
57		2		3	1
58	1			1	
59	3	1	2		
60	3	3			
61	2	1			
62			1	1	
63				3	2
64			2	3	2
65	3	2	1		
66				2	4
67	3	4			
68		1	4		
69		2	3	2	2
70	2		1		
71		3		3	
# chicks	75	91	48	89	62
# nests	33	45	25	39	26

Table 4. Yearly estimates of genetic diversity and effective population size over all loci (see abbreviations from Table 1). *n* = number of sampled individuals, H_O = observed heterozygosity, H_E = expected heterozygosity, *A* = number of alleles, *AR* = allelic richness, F_{IS} = inbreeding coefficient (*P* < 0.05 in bold) and N_e = effective population size with 95% confidence limits in parentheses.

	n	H_O	H_E	*A*	*AR*	F_{IS}	N_e (*95% CL*)
2006	57	0.5548	0.5698	5.20	5.18	0.0263	83 (71.6–113.9)
2007	68	0.5640	0.5840	5.40	5.39	0.0343	81 (67.8–120.2)
2008	27	0.5506	0.5990	4.70	4.66	0.080	31 (27.9–38.2)
2009	58	0.5518	0.5887	5.20	5.20	0.0627	82 (70.2–113.9)
2010	33	0.5521	0.5762	4.80	4.76	0.0418	41 (35.8–48.5)

FIGURE LEGENDS

Figure 1. Peregrine Falcon sampling sites across years 2006-10.

Figure 2. Mean relatedness and *SD* of a) between siblings from the same nest, territory and year, b) between chicks from nests within the same territory but different years, and c) between chicks from nests below the cut-off value of 0.297 (= likely turnover of parent(-s)). *** = significant difference at $P < 0.01$.

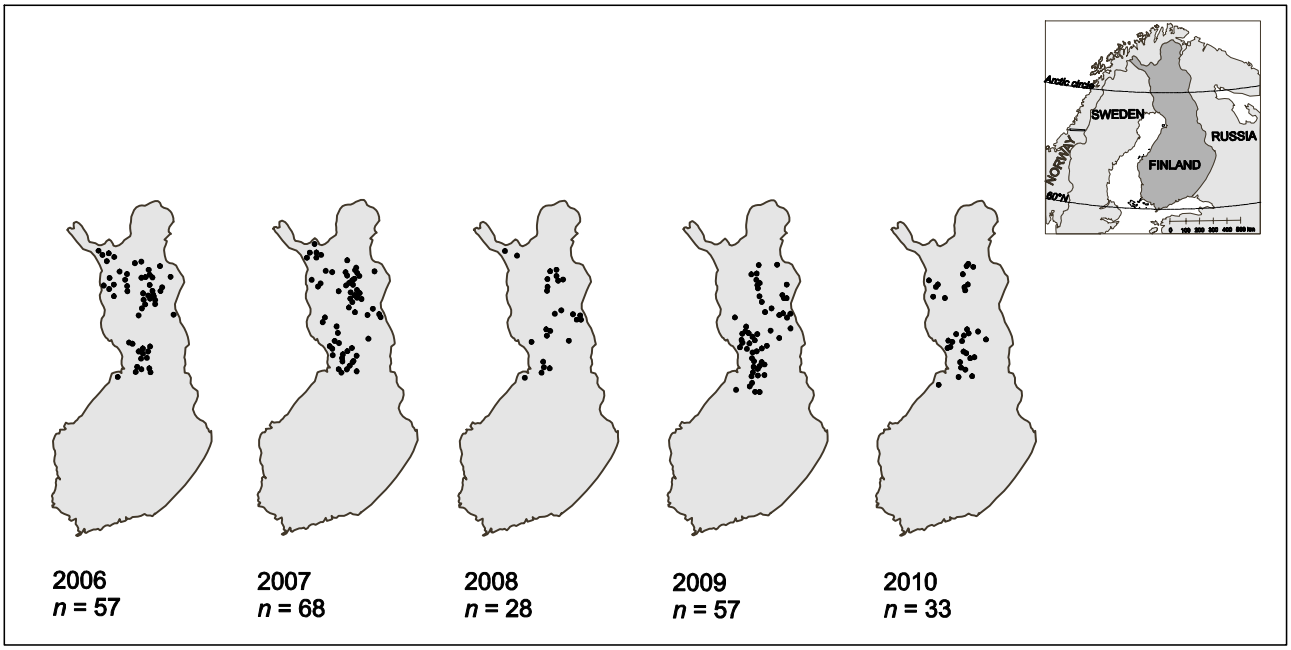
SWEDEN
RUSSIA
FINLAND
NORWAY
Arctic circle
60°N
2006
n = 57
2007
n = 68
2008
n = 28
2009
n = 57
2010
n = 33

Figure 1.

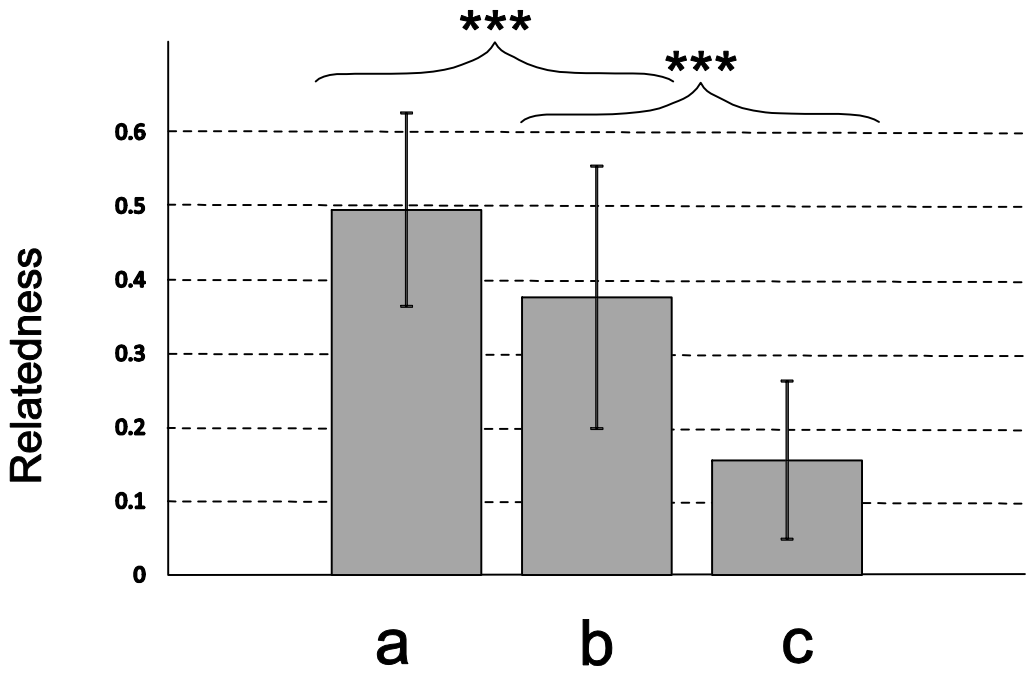

Figure 2.