Long-distance dispersal in migratory pied flycatchers *Ficedula hypoleuca* is relatively common between the UK and the Netherlands

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Long-distance dispersal can potentially have important consequences for evolutionary change, but is difficult to quantify. We present quantitative estimates of natal dispersal between the UK and the Netherlands in a long-distance migratory bird, the pied flycatcher. Due to over 90 000 individual ringed adults caught and 730 000 ringed nestlings we are able to estimate that dispersal of young born in the UK to breeding in the Netherlands occurs on average 43 times yr^{-1}, and probably even more recently. We estimated that between 2000 and 2009 about 0.70% of the Dutch adult population could be immigrants from the UK. No cases of dispersal from the Netherlands to the UK were observed. Dispersing individuals bring new genes to the Netherlands, as males in the UK have a darker plumage than Dutch males. We found a good qualitative match between the proportion of dark males breeding in two Dutch populations and the estimated immigration rate from the UK. This and potentially other genetic differences may allow for new evolutionary directions if these genes are beneficial in the new population. The causes of dispersal are unknown, but it is striking that especially birds from the northern range limit dispersed.

Dispersal is a key process in evolution and ecology, because it enables genetic exchange between populations, and hence may change levels of local adaptation, facilitate the introduction of new genes into populations, and allow individuals to escape from sites with low reproductive potential.

Dispersal is ubiquitous in most populations, but is difficult to quantify because individuals cannot be easily tracked when dispersing further away from their natal site, i.e. outside the study area (Thomson et al. 2003). Therefore most dispersal studies focus on local dispersal between study plots (Van Der Jeugd 2001, Doligez et al. 2002, Tinbergen 2005, Parn et al. 2009), and ignore longer distance dispersal (Winkler et al. 2004). Long distance dispersal can only rarely be quantified directly (Van Der Jeugd and Litvin 2006), but new techniques like stable isotope ratios (Hobson 2005, Studds et al. 2008) or genetic markers (Hansson et al. 2004, Knudsen et al. 2011) may allow its estimation. In this paper we make use of a well-studied species, the pied flycatcher *Ficedula hypoleuca*, to quantitatively estimate long-distance dispersal from direct observations and detection probabilities (Thomson et al. 2003, Winkler et al. 2004, Korner-Nievergelt et al. 2010) using data from the Netherlands and the UK.

Several long-distance migratory passerines show little geographic neutral genetic variation over vast areas (Lehtonen et al. 2009, Santure et al. 2010), suggesting that dispersal may be prevalent, yet mean observed dispersal distances are typically small (Paradis et al. 1998). For pied flycatchers the mean natal dispersal distance from UK ring recoveries was 20 km (Paradis et al. 1998), whereas dispersal rates corrected for capture probability showed that 31% of Dutch pied flycatchers dispersed < 10 km, 56% between 10 and 50 km, and 13% between 50 and 100 km (Thomson et al. 2003). Mean dispersal distances are important for estimating individual fitness or survival, but from an evolutionary viewpoint the tail of the distribution may be more interesting, as long-distance dispersers are likely to introduce new genetic material to distant populations. In the case of pied flycatchers we examine a single genetic trait, male plumage colouration, that differs markedly between the UK and the Netherlands (Lundberg and Alatalo 1992), and therefore can be used to show the potential importance of long-distance dispersal in changing the genetic composition of populations.

Methods

Pied flycatchers are ringed in large numbers in both the Netherlands (NL) and the UK, and for this reason we use

this species to calculate dispersal rates between these two countries. This bird is a long-distance migrant, spending the winter in western Africa. Between 1970 and 2009 about 250 000 nestling and about 30 000 breeding adult pied flycatchers have been ringed in NL and about 480 000 nestlings and 60 000 breeding adults in UK. The sex ratio of ringed adults is only known for NL between 1991 and 2009, with 17% of captured breeding adults being male as females are more easily caught during incubation (databases from Dutch Centre for Avian Migration and Demography and the British Trust for Ornithology).

We estimated detection rates of dispersing individuals based on the proportion that a young bird is ringed in one country and is recaptured as a breeding adult in the other country ($p_{ring, x} \times p_{recapt, y}$). Ringing probability of nestlings was the number of nestlings ringed in any year divided by the breeding population estimate in that year multiplied by the mean brood size of five fledglings. Population estimates were taken from the most recent breeding atlases (Gibbons et al. 1993, SOVON Vogelonderzoek Nederland 2002) incorporating trends from annual common bird census data (Table 1). For the Netherlands we used the common bird census data as indexed by SOVON (< www.sovon.nl/ soorten.asp?euring = 13490&lang = nl >) from 1990 to 2009 and the most recent estimate of the breeding population of 16 000 pairs in 1999 (SOVON Vogelonderzoek Nederland 2002). For the UK we used the Breeding Bird Survey data from 1994 to 2009 (Baillie et al. 2001) and the population estimate of 31 600 pairs in 2000 (Wernham et al. 2002). The yearly population size in year t was the index of t divided by the index in the reference year, times the number in the reference year. The probability of a breeding adult being caught in its lifetime was based on the number of newly ringed breeders every year, and assuming an adult survival rate of 50% (Sanz 2001). This may be on the high side, but this makes our estimates of dispersal conservative (Chernetsov et al. 2009). Given these data, we calculated the annual number of ringed adults still alive (= newly ringed + survival × number of ringed breeders from previous years), and divided this by the estimated population size to arrive at the proportion of the total population for which the adult identity was known. For each year we calculated the proportion of ringed adults still alive, and averaged these proportions for all years for which we had good estimates on both population sizes and number of ringed adults (1990–2009). We assume that this proportion was not dramatically different before this period, but we lack good estimates of population sizes for this period. The estimated number of dispersers is the actually observed number divided by the detection rate. The uncertainty in these estimates is not due to ringing and catching effort because these are high in comparison to most other species, but in the low

chance of actually capturing an individual that dispersed between countries. To give some notion about the effect of chance, we also calculated annual estimates of dispersal rate with −1 or +1 number of actually observed dispersers.

We also estimated the proportional contribution of UK birds to the Dutch breeding population by assuming that half of the adult breeders must be replaced by young individuals each year (given the survival rate of 50%), and divide the annual estimated number of UK recruits by the annual number of new recruits. This calculation was only done for 2000–2009, because estimates before 1990 of population sizes were less reliable, and between 1990 and 1999 no UK recruits were reported.

A comparison between the observed Dutch plumage colour scores (named: Drost scores) and the UK scores is based on a population in Cumbria (Lundberg and Alatalo 1992, their Fig. 68; most UK birds found in NL originated from that region) and on two populations in NL (Hoge Veluwe (2000–2003) and Drenthe (2007–2010)) where UK male dispersers have been caught. Colour scores run from 1 for males with completely black dorsal parts to 7 with completely brown dorsal parts (Drost 1936).

Results

Eight cases of natal dispersal from UK to NL have been recorded, but none in the opposite direction despite similar proportions of young and adult birds being ringed (Table 1). The mean distance between ringing and recapture was 628 km (range 574–660 km). Five of the eight cases refer to live recaptures of adults (three males, two females) during the breeding season in a nest box. The remaining three birds were found dead during the breeding season in suitable habitat, and their sexes were unknown. Below we only consider live recaptures in our estimations, because only for those we can calculate capture probabilities. One of dispersal cases was recorded in the 1970s (live), three in the 1980s (one live, two death) and four in the 2000s (three live and one death). One case of breeding dispersal was observed: a female bred in 1987 in Scotland near Stirling, and was recaptured in 1989 breeding in the NL near Nunspeet (793 km).

The likelihood of detecting natal dispersal based only on live recaptures from the UK to NL was 0.29% (i.e. proportion of nestlings being ringed in the UK (0.0948) multiplied by the proportion of caught adults in NL being ringed (0.0306), Table 1). This results in an estimated 1724 (= 5/0.0029) dispersed individuals between 1970 and 2009: 43 individuals yr^{-1}. To give some confidence interval around this estimate, the annual number of dispersers would have been 35 if we had caught four dispersing individuals, and 52 if we had caught six. Three of the five recaptured birds

Table 1. Estimates of numbers and ringing proportions for pied flycatchers in the UK and in the Netherlands. All estimates are yr^{-1}.

Country	Breeding population size yr^{-1}	Estimated number fledglings yr^{-1}	Avg num ringed fledglings yr^{-1} (1970–2007)	Avg num newly ringed adult yr^{-1} (1970–2007)	Proportion juveniles ringed	Proportion adults ringed
UK	31 650 (88-91)	158 250	15 000	1698	0.0948	0.0450[1]
NL	16 500 (98-00)	82 500	6491	522	0.0787	0.0306[1]

[1]This is the average of the annual proportions of ringed adults estimated to be alive in a year.

occurred in the period 2000–2009, which would rather imply 1124 cases in total, or 112 individuals yr^{-1} and may suggest an increased dispersal rate (with two observed dispersal events this would be 765, and with four 1530 individuals yr^{-1}). Given the Dutch population size, this would account for 0.7% of the breeding population with an UK origin (for 2000–2009).

The detection rate for a young bird ringed in NL to be caught breeding in the UK would be 0.35%. The apparent lack of natal dispersal from NL to the UK is not due to a lower detection rate, but possibly be due to the smaller (source) population size in NL.

Interestingly, all UK immigrants since 2000 originated from a rather small area near the northern edge of the range for which recoveries occur, and dispersal distances for these birds were about 650 km between natal and breeding sites (Fig. 1, difference in latitude alone is ca 160 km). This concentration does not match the ringing or breeding distribution of the species, which is biased towards Wales (Gibbons et al. 1993, Wernham et al. 2002). If we compare the ringing latitude of pied flycatcher chicks ringed in the UK and recovered in the Mediterranean region during spring migration (assuming this is a random sample of the population) (mean 52.57°, SE 0.13, n = 120) with the birds that dispersed to NL (mean 53.96°, SE 0.36, n = 8), there is a clear difference (Wilcoxon Rank sum test, U = 778, p = 0.003).

Male breeding birds in NL have a predominantly brownish plumage, contrasting with the predominantly blackish plumage of UK breeding birds (Fig. 2). The two UK males breeding in NL with known plumage score resembled UK colour scores (i.e. Drost 2 and 3). Since colour score is highly heritable ($h^2 = 0.50$ for UK (Lundberg and Alatalo 1992)), and the Dutch population carries mostly genes for males at the brown end of the spectrum, one could speculate that males with colour scores 2 and 3 may have a UK origin: they would only arise from pairs for which both members would carry these dark alleles, an unlikely event in the resident Dutch population. If so, about 3% of the current Dutch (male) population might be of British origin. We estimated the immigration rate for UK flycatchers in the Dutch population for 2000–2009 as being 0.7% for both sexes together (see above), but if we restrict the estimate for males this rises to 2.4% because of the lower recapture rate of males. This percentage is surprisingly close to the percentage of 3% of dark male colour morphs breeding in recent years.

Discussion

Pied flycatcher natal dispersal between UK and NL is not commonly observed, but, taking detection rates into account, is likely to occur frequently. We acknowledge our estimates must have large confidence intervals, because they are based on few recaptures (but with enormous sample sizes). Nevertheless, these data strongly suggest that long-distance dispersal is more common than often thought, and may be biased from the island population to the mainland
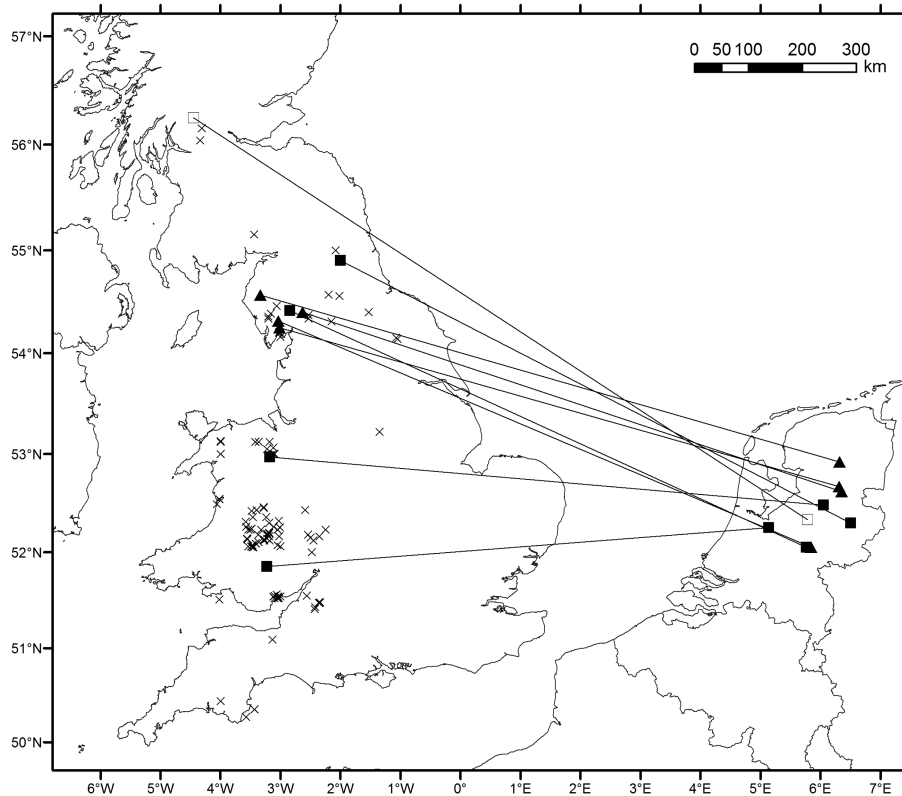

Figure 1. Dispersal of pied flycatchers ringed in UK as nestlings (filled symbols) or breeding adults (open symbols) from UK to NL during the period 1970–2000 (squares) and 2000–2009 (triangles). Both death and live reports of dispersing individuals are plotted. Small crosses indicate ringing locations of birds recovered during spring migration in the Mediterranean. No cases of dispersal from the NL to UK were reported.
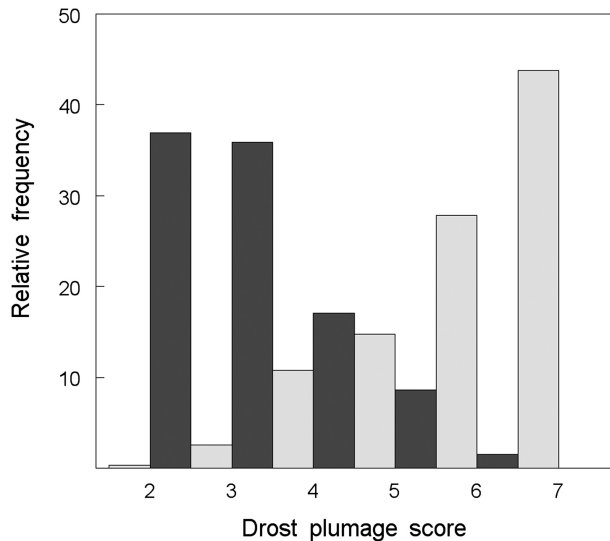
Figure 2. Frequency distribution of pied flycatcher male plumage score according to Drost (1936) in two populations in NL (light) where males of UK origin have been found (n = 863), and in Cumbria (dark, n = 489, (Lundberg and Alatalo 1992)). The two immigrant males in NL had scores of 2 and 3. Scores range from 1 (completely black dorsal parts) to 7 (completely brown dorsal parts).

rather than in opposite direction. These high levels of dispersal are consistent with low (but significant) levels of neutral genetic differentiation between UK and NL (Lehtonen et al. 2012), although dispersal may introduce new functional genes on which selection can act (see below).

Dispersal is mostly female-biased in passerines, but our data on long-distance dispersal suggest the opposite: 83% of all NL captures were females, but three dispersing UK males were caught in NL and only two females. A potential capture bias through ringers focusing on rare dark males in the population, hence selectively catching UK males, seems unlikely however, since two of the three males were captured as part of an intensive population monitoring scheme, where all males were caught.

The reported high rates of immigration may result in a change in gene frequencies, at least for male plumage colouration. Limited historical data on plumage colour from the Dutch population in the early 1970s found a single dark male (Drost 2) among 77 males of colour scores 5 and higher (Haverschmidt 1973). At present, we find more dark males, and this change has mostly occurred since the mid-1990s (Both unpubl.). It is suggestive that the proportion of dark males (Drost 2–3) in our populations and the calculated proportion of UK immigrant males match quite well, which could mean that a change in colour morphs reflects increased immigration rates (gene flow), rather than a selective advantage of dark males.

Long-distance dispersal in long-distance migrants can easily be explained by settlement following slight navigational errors, especially in the case of birds missing the passage to an island. However, also on the mainland long-distance dispersal may be a general phenomenon which can explain the observed low levels of neutral genetic diversity in this and other migrant species (Lehtonen et al. 2009,

Santure et al. 2010). In times of large-scale environmental change, species may need to adapt by an evolutionary response and at present the potential for this is mostly investigated by considering the additive genetic variation within populations (Visser 2008). As we have shown, dispersing individuals add new genetic variation to distant populations, and thereby allow for new evolutionary directions (Both 2012).

References

Baillie, S. R., Crick, H. Q. P., Balmer, D. E., Bashford, R. I., Beaven, L. P., Freeman, S. N., Marchant, J. H., Noble, D. G., Raven, M. J., Siriwardena, G. M., Thewlis, R. and Wernham, C. V. 2001. Breeding birds in the Wider Countryside: their conservation status 2000. – Research Report 252, BTO, Thetford.

Both, C. 2012. Implications of climate change for habitat use by birds. – In: Fuller, R. A. (ed.), Birds and habitat: relationships in a changing landscape. Cambridge Univ. Press, in press.

Chernetsov, N., Sokolov, L. V. and Kosarev, V. 2009. Local survival rates of pied flycatchers *Ficedula hypoleuca* depend on their immigration status. – Avian Ecol. Behav. 16: 11–20.

Doligez, B., Danchin, E. and Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. – Science 297: 1168–1170.

Drost, R. 1936. Ueber das Brutkleid maennlicher Trauerfliegenfaenger. – Vogelzug 7: 179–186.

Gibbons, D. W., Reid, J. B. and Chapman, R. A. (eds) 1993. The new atlas of breeding birds in Britain and Ireland: 1988–1991. – T and AD Poyser.

Hansson, B., Bensch, S. and Hasselquist, D. 2004. Lifetime fitness of short- and long-distance dispersing great reed warblers. – Evolution 58: 2546–2557.

Haverschmidt, F. 1973. Waarnemingen aan een populatie bonte vliegenvangers *Ficedula hypoleuca*. – Limosa 46: 1–20.

Hobson, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. – Divers. Distrib. 11: 157–164.

Knudsen, E., Linden, A., Both, C., Jonzen, N., Pulido, F., Saino, N., Sutherland, W. J., Bach, L. A., Coppack, T., Ergon, T., Gienapp, P., Gill, J. A., Gordo, O., Hedenstrom, A., Lehikoinen, E., Marra, P. P., Moller, A. P., Nilsson, A. L. K., Peron, G., Ranta, E., Rubolini, D., Sparks, T. H., Spina, F., Studds, C. E., Saether, S. A., Tryjanowksi, P. and Stenseth, N. C. 2011. Challenging claims in the study of migratory birds and climate change. – Biol. Rev. 86: 928–946.

Korner-Nievergelt, F., Sauter, A., Atkinson, P. W., Guelat, J., Kania, W., Kery, M., Koppen, U., Robinson, R. A., Schaub, M., Thorup, K., van der Jeugd, H. and van Noordwijk, A. J. 2010. Improving the analysis of movement data from marked individuals through explicit estimation of observer heterogeneity. – J. Avian Biol. 41: 8–17.

Lehtonen, P. K., Laaksonen, T., Artemyev, A. A., Belskii, E., Both, C., Bures, S., Bushuev, A. V., Krams, I., Moreno, J., Magi, M., Nord, A., Potti, J., Ravussin, P.-A., Sirkiä, P. M., Saetre, G. P. and Primmer, C. R. 2009. Geographic patterns of genetic differentiation and plumage colour variation are

different in the pied flycatcher (*Ficedula hypoleuca*). – Mol. Ecol. 18: 4463–4476.

Lehtonen, P. K., Laaksonen, T., Artemyev, A. A., Belskii, E., Berg, P. R., Both, C., Buggiotti, L., Bures, S., Burgess, M. D., Bushuev, A. V., Krams, I., Moreno, J., Magi, M., Nord, A., Potti, J., Ravussin, P.-A., Sirkiä, P. M., Saetre, G. P., Winkel, W. and Primmer, C. R. 2012. Candidate genes for colour and vision exhibit signals of selection across the pied flycatcher (*Ficedula hypoleuca*) breeding range. – Heredity 108: 431–440.

Lundberg, A. and Alatalo, R. V. 1992. The pied flycatcher. – T and AD Poyser.

Paradis, E., Baillie, S. R., Sutherland, W. J. and Gregory, R. D. 1998. Patterns of natal and breeding dispersal in birds. – J. Anim. Ecol. 67: 518–536.

Parn, H., Jensen, H., Ringsby, T. H. and Saether, B. E. 2009. Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. – J. Anim. Ecol. 78: 1216–1225.

Santure, A. W., Ewen, J. G., Sicard, D., Roff, D. A. and Moller, A. P. 2010. Population structure in the barn swallow, *Hirundo rustica*: a comparison between neutral DNA markers and quantitative traits. – Biol. J. Linn. Soc. 99: 306–314.

Sanz, J. J. 2001. Latitudinal variation in female local return rates in the philopatric pied flycatcher (*Ficedula hypoleuca*). – Auk 118: 539–543.

SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse broedvogels; verspreiding, aantallen, verandering – Nederlandse Fauna 5. – Naturalis, KNNV Uitgeverij and EIS-Nederland, Leiden.

Studds, C. E., Kyser, T. K. and Marra, P. P. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. – Proc. Natl Acad. Sci. USA 105: 2929–2933.

Thomson, D. L., van Noordwijk, A. and Hagemeijer, W. 2003. Estimating avian dispersal distances from data on ringed birds. – J. Appl. Stat. 30: 1003–1008.

Tinbergen, J. M. 2005. Biased estimates of fitness consequences of brood size manipulation through correlated effects on natal dispersal. – J. Anim. Ecol. 74: 1112–1120.

Van der Jeugd, H. P. 2001. Large barnacle goose males can overcome the social costs of natal dispersal. – Behav. Ecol. 12: 275–282.

Van der Jeugd, H. P. and Litvin, K. Y. 2006. Travels and traditions: long-distance dispersal in the barnacle goose *Branta leucopsis* based on individual case histories. – Ardea 94: 421–432.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. – Proc. R. Soc. B 275: 649–659.

Wernham, C. V., Toms, M., Marchant, J. H., Clark, J., Siriwardena, G. M. and Baillie, S. R. 2002. The migration atlas: movements of the birds of Britain and Ireland. – T and AD Poyser.

Winkler, D. W., Wrege, P. H., Allen, P. E., Kast, T. L., Senesac, P., Wasson, M. F., Llambias, P. E., Ferretti, V. and Sullivan, P. J. 2004. Breeding dispersal and philopatry in the tree swallow. – Condor 106: 768–776.