Pied Flycatcher *Ficedula hypoleuca* population dynamics in peripheral habitats in Scandinavia

Per Gustav Thingstad[1,*], N. Erik I. Nyholm[2] & Bent Fjeldheim[3]

Local populations in marginal habitats close to the distribution border are expected to vary more in size than central populations. To obtain information on the viability of metapopulations, monitoring in peripheral habitats might therefore be an effective way. To test this hypothesis we analysed breeding success and fluctuations in population size of Pied Flycatcher *Ficedula hypoleuca* in three subalpine forests in Scandinavia, each representing a peripheral habitat (in southern Norway, Hemsedal, in central Norway, Lierne, and in northern Sweden, Ammarnäs). Data were collected in the period 1986–2005. Numbers of flycatchers in these habitats in Fennoscandia have been increasing for decades, but since the 1970s negative trends are observed. This study showed that the populations breeding in Lierne and Ammarnäs exhibited demographic characteristics that are typical for a sink population, i.e. large annual variation in recruitment, which was on average insufficient to maintain population size; in contrast Hemsedal seemed to function as a source population. The decrease in population size since the start of this survey was most evident for the two sink populations. Weather conditions at the flycatcher's wintering areas in western Africa were suspected to be responsible for the decrease, at least there were no indications of any climatic change at the breeding grounds. However, the breeding success of the sink populations was significantly correlated to June temperatures. During the last years of the study, all three populations seemed to recover. This recovery was most pronounced for the source population in Hemsedal while the other two populations showed some time-lag. As an index of the Fennoscandian population size of Pied Flycatcher we used catch data in autumn from three ringing stations in southern Scandinavia. The numbers of initiated clutches in our populations were correlated with this index from the previous autumn, supporting the idea that populations in peripheral habitats are sensitive yardsticks for overall population size. Similarly, the numbers of successful clutches in our two populations with low predation rate were positively related to the same index. Taken together, our three border populations are considered good indicators for the overall population trend in Fennoscandia.

Key words: Pied Flycatcher, border population dynamics, source and sink, long-term study, weather influence

[1]Museum of Natural History and Archaeology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway;
[2]Department of Ecology and Environmental Science, Umeå University, S-901 87 Umeå, Sweden (erik.nyholm@eg.umu.se);
[3]NO-3560 Hemsedal, Norway;
[*]corresponding author (per.thingstad@vm.ntnu.no)

INTRODUCTION

Abiotic factors, such as climatic conditions, are known to have more effect on demographic parameters in peripheral than in central areas (Hoffmann & Blows 1994, García & Arroyo 2001, Sanz 2003). Accordingly, populations tend to concentrate more toward the core areas when experiencing bad conditions, e.g. during years with adverse weather, and population declines will be most pronounced within boundary areas (Mehlman 1997). The Pied Flycatcher *Ficedula hypoleuca* is one of the passerine species facing strong declines in numbers during the last decades (Lundberg 1997). Within the European distribution range, the Scandinavian subalpine forests form peripheral habitats, which were colonised relatively recently. This raises the question how the flycatcher populations in these marginal habitats behave during a period of population decline.

After the last glaciation the Pied Flycatcher has probably followed the northern expansion of the deciduous forest in Europe (Sætre *et al.* 2001), where it mainly breeds in temperate, but also in boreal zones (Cramp & Perrins 1993). However, historical information suggests that it spread across Europe from southwest toward northeast as late as since the early 1800s (Lundberg & Alatalo 1992). Today it is most commonly breeding in Fennoscandia, the Baltic countries, Belarus and Russia, less so in West Europe and markedly scarcer in Central, South and South-East Europe (Lundberg 1997). In most of Europe it appears as a long-distance migrant, wintering south of Sahara in West Africa (Cramp & Perrins 1993). In the 1950s and 1960s, the Pied Flycatcher was reported expanding in northern Norway (Haftorn 1957) and in northern Finland, where the first record was done in summer 1954 (Järvinen 1983). During that period it became more abundant in the subalpine birch forests of the mountain areas of southern Norway (Haftorn 1971). After a period of rapid growth in the subalpine breeding populations of this 'southern newcomer' in Fennoscandia (Järvinen 1983), a shift toward decreasing trends have been registered in several local populations (Enemar *et al.* 1984, 2004, Thingstad & Fjeldheim 1999).

Some of the causes for the prolonged reduction in population size might be found outside the breeding areas, e.g. migrating bird species are susceptible to shifts in large-scale climatic patterns (Sillett *et al.* 2000, Sæther 2000). In addition, annual variations in weather conditions in the breeding grounds cause fluctuations in the size of local populations and modulate long-term trends (Järvinen & Väisänen 1984, Lundberg & Alatalo 1992, Thingstad 1997).

The Pied Flycatcher can breed in a broad variety of forest habitats of varying suitability, between which dispersal is possible. The source–sink model (Murphy 2001) is one of the ways to understand population dynamics. This theory implies that some populations produce more recruits than needed to cover mortality and population growth ('source') and others where annual losses exceed local recruitment and numbers are maintained by immigration from elsewhere ('sink'). Sink habitats might have positive effects on the overall population if they serve as temporary patches where individuals await their opportunities to disperse back to source habitats, or negative effects if they attract individuals from better habitats (Howe *et al.* 1991, Gaona *et al.* 1998).

During a period of 20 years we collected information on population dynamics in three widely separated populations of Pied Flycatcher in the Scandinavian subalpine forest region. Because of the large range in geographical positions we expected that the breeding conditions, and thereby the population dynamics, would differ considerably among the study populations. In the first place, we investigated whether we could apply the 'source–sink'-hypothesis to the study populations. Secondly, we aimed to explain variation in population parameters by climatic conditions, which we did by exploring both effects of weather in the breeding sites and effects of weather in the wintering range. In particular, we asked if climatic effects differed for source and sink populations. Thirdly, we explored to which extent variation in the local population sizes was related to the total

Scandinavian population. We estimated total population size using numbers of captures of flycatchers at migration observatories in southern Scandinavia during autumn migration.

MATERIAL AND METHODS

Study areas

The study areas were located within the subalpine birch forest region in southern and central Norway (Hemsedal and Lierne, respectively) and in Swedish Lapland (Ammarnäs) (Fig. 1). The area in Hemsedal (60º52'N, 8º32'E) was located at 700–750 m above sea level (a.s.l.) in a birch *Betula* sp. forest mixed with spruce *Picea* sp., aspen *Populus* sp. and rowan *Sorbus* sp. and contained 51–65 nestboxes (on average 63), more or less randomly spaced out in the forest. The forest was grazed by cattle, which might attract insects. In addition some of the forest was fertilised by manure. In Hemsedal mean long-term temperatures in June and July are about 10 and 11ºC, respectively.

In Lierne (64º20'N, 13º45'E) the number of available nestboxes varied between 126 and 150 during the study period (on average 141). The boxes were located in two transects, separated by a distance of 400–1500 m, on a north-east-facing slope in a 'heath birch forest' covered by birches with spruce and rowan (Fig. 2). The lowest transect was located close to a lake at 540–545 m a.s.l., while the other was more sheltered in the forest at 600–680 m a.s.l. Some of the nestboxes were located in edges toward bogs, and some of those in the upper transect were close to the tree line. In Lierne the mean temperatures in June and July are about 8 and 10 ºC, respectively.

The 218 nestboxes in Ammarnäs (65º58'N, 16º13'E) were located 530–640 m a.s.l. in a south-facing slope of the mountains Gaisatjåkke and Valle. The forests were predominantly rich meadow birch forests, and the temperature conditions were fairly identical to those in Hemsedal. Pied Flycatcher nests were frequently depredated by small mustelids during the study period. From

Figure 1. Map showing the locations of the three study areas.

being a rather rare event during 1965–1986, the predation was consistently more frequent during 1987–2005 (on average 5 and 35.8%, respectively, of the initiated clutches). The depredated nests were included in the calculation of initiated clutches and mean clutch size, but were omitted from the calculations of successful clutches. This approach was also applied to the very few depredated clutches in Hemsedal and Lierne.

June is the most critical month for the breeding progress. Accordingly, the deviations from the normal (1961–1990) June temperatures (given in 0.5°C intervals) during the actual 20-year period were obtained from the nearest Norwegian meteorological stations (Geilo, Lierne and Øvre Saltdal).

Figure 2. View on the mountain forest of the study area in Lierne, Norway (photo P.G. Thingstad).

Data collection

The nestboxes were of the standard Great Tit *Parus major/*Pied Flycatcher-type, and were separated by a distance of at least 30 m. Each nestbox was visited at least three times during the breeding season in Lierne and at least four times (usually five to ten times) in Ammarnäs and Hemsedal to count the total number of eggs, numbers hatched and unhatched, and living and dead nestlings. In our three study areas the Pied Flycatcher was the most abundant breeding species in the nestboxes, and therefore competition with other species was expected to be minimal. There was a surplus of nestboxes in the three study areas; therefore we expect no significant effect on the collected demographic parameters due to the differences in number of available nestboxes (cf. Virolainen 1984). Hemsedal had fewest nestboxes, and was probably the most densely packed area. The number of available nestboxes and their occupation rate varied considerably between the study areas. On average 12% of the nestboxes were occupied in Lierne, 34% in Ammarnäs and 57% in Hemsedal. Accordingly, if there would be any density-dependent factor involved this should be most noticeable in the latter area.

Data collected were the number of clutches initiated (number of eggs ≥ 1), number of eggs in complete clutches (defined as clutches containing at least 3 eggs, as those containing less almost always were abandoned), number of eggs hatched, number of successful clutches (at least one fledged young), number of fledglings in successful clutches, and number of deserted or predated clutches (the entire clutch was always depredated in these cases). Breeding success was calculated as the percentage of eggs that produced fledged young. Because the occupation rate of nestboxes and the way they were spaced out in the area differed among study sites, some of our demographic

parameters were standardised as numbers per 100 available nestboxes. Due to the short breeding season in our subalpine habitats replacement of clutches occurs rarely, and the few replaced clutches – unsuccessful in all cases – have not been included in our material.

To arrive at an index for the population size in autumn data from more or less standardised ringing activities from three southern Scandinavian ringing stations (Falsterbo, Lista and Jomfruland) were used. The mean number of ringed Pied Flycatchers during the 10-year period 1990–99 at each of the three stations was calculated, and subsequently the annual numbers of ringed individuals were expressed as a ratio to this average. Finally, the mean of the three ratios, multiplied by 100, was used as an annual index. For some years, means were based on data from two stations only; for Lista the years 1986–1989 were missing, and for Jomfruland (obtained from Figure 7 in Edvardsen *et al.* 2004) the three last seasons.

For statistical tests SPSS package version 13.0 was used. To find the best-fit models for the revealed trends a curve estimation procedure was run. This procedure allows us to examine the relationships between one or more independent variables and one dependent variable, and fits curves to time series. The curves were selected from 11 available regression models. The criterion used for selecting the best-fitting model was the overall *F*-test; the model with the highest *F*-value was selected. In analyses of correlation, Spearman correlation coefficient r_s or Pearson correlation coefficient r was calculated.

RESULTS

Demographic parameters

During 1986–2005 the flycatcher's populations had varying success in producing fledglings in the three study areas. The mean annual number of fledglings produced by each pair was almost consistently highest in Hemsedal (Fig. 3A). For self-maintenance of local Fennoscandian populations at least 4.4 young should be produced per com-
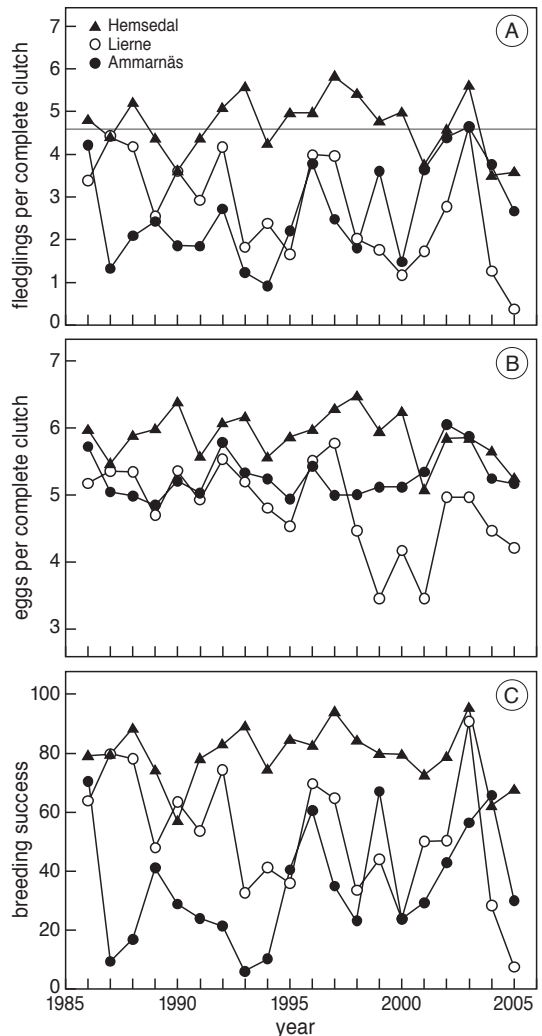

Figure 3. Breeding parameters in Hemsedal, Lierne and Ammarnäs during the study period. (A) Mean number of fledglings in complete clutches (number of eggs ≥ 3). The dotted line represent the self-maintenance level of the populations according to Järvinen (1983). (B) Mean number of eggs in complete clutches. (C) Breeding success as percentage of eggs producing fledged young.

pleted clutch (failed complete clutches included; Järvinen 1983). For most of the years the young production in Hemsedal was above this critical value. On average 4.7 fledglings were produced in complete clutches, and 5.2 in the successful

clutches. In particular in 2004 and 2005 production was low. Although Hemsedals production was only slightly higher than the critical value, it produced a surplus of young in most of the years. We therefore consider Hemsedal as a source habitat. In contrast, production of fledglings in Lierne and Ammarnäs was considerably lower (2.8 and 2.7 for complete clutches, and 3.9 and 4.3 for successful clutches). As production was well below Järvinen's (1983) threshold we consider these two areas to hold sink populations.

The mean number of eggs laid in complete clutches was relatively stable during the study period, except for drops in 1998–2001 and 2004–2005 in Lierne (Fig. 3B). In Hemsedal complete clutches contained on average 5.9 eggs, in Lierne and Ammarnäs 4.9 and 5.3 eggs, respectively. In each of the study areas, the mean number of eggs per year correlated significantly with the number of fledged young in complete broods (Lierne $r_s = 0.81$, $P < 0.001$, Ammarnäs $r_s = 0.54$, $P < 0.05$, and Hemsedal $r_s = 0.55$, $P < 0.05$).

The numbers of initiated clutches in Lierne and Ammarnäs were correlated to each other ($r_s = 0.71$, $P = 0.001$), but none was correlated to the numbers of the Hemsedal population ($r_s = 0.35$ and $r_s = 0.30$, respectively). This suggests that numbers of breeders fluctuated synchronously in Lierne and Ammarnäs, while population size in Hemsedal behaved differently.

Breeding success was consistently high in Hemsedal (mean = 79.1%), and considerably lower in Ammarnäs (mean = 36.0%) and Lierne (mean = 51.7%) (Fig. 3C). One of the reasons for the low success in Ammarnäs was most probably the high predation rate, which resulted in depreda-tion losses varying from 3% (in 1986) to as much as 64% of the initiated clutches. Consequently, the mean numbers of produced fledglings in initiated clutches were negatively correlated with the annual predation rate ($r_s = -0.79$, $P < 0.001$).

The demographic parameters of the Hemsedal population showed a considerably lower coefficient of variation than the populations in Lierne and Ammarnäs (Table 1).

Response to climate
The registered long-term decline of the Pied Flycatcher since the 1970s coincided with the long-lasting dry spell period in Sahel, which we think is representative for the wintering conditions of the species (Fig. 4). However, during our study
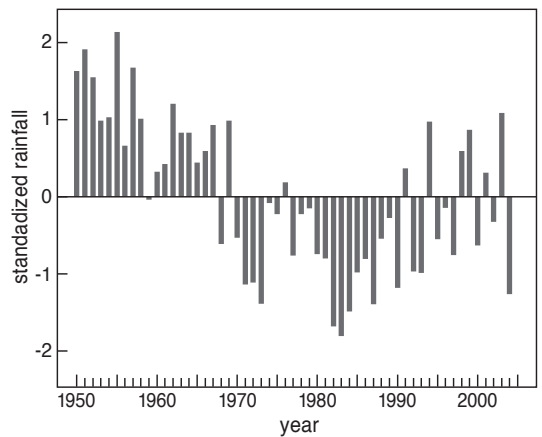

Figure 4. Rainfall in the Sahel (June through October) during the period 1950–2004. The rainy season is cent-red in July–September. Averages were standardized to mean = 0 and SD = 1.
Data are from http://jisao.washington.edu/data/sahel.

Table 1. Coefficient of variation for reproduction parameters during the study period (complete clutches only).

	Number initiated clutches	Number successful clutches	Number eggs	Number fledglings	Mean number eggs	Mean number fledglings	Breeding success
Hemsedal	17.6	17.3	17.7	17.2	6.1	15.1	12.4
Lierne	59.1	82.4	69.9	97.8	13.2	45.3	41.2
Ammarnäs	33.7	76.5	40.3	86.7	6.3	41.6	55.1

period the annual fluctuations in size of the three local breeding populations did not follow the Sahel rainfall index. In fact in our areas the numbers of initiated clutches were negatively correlated, though not significantly, with the Sahel rainfall index during the previous season ($r_s = -0.37$, -0.43 and -0.21 for Lierne, Ammarnäs and Hemsedal, respectively).

The breeding success was significantly correlated with mean June temperatures in Lierne and Ammarnäs, but not so in Hemsedal (Fig. 5). During the study period temperature conditions in the study areas remained more or less stable.

Time-lag response

The number of young produced correlated positively with the number of clutches that were established the following year (year x+1; Table 2). However, this relationship was only significant for Hemsedal and Lierne. As a large proportion of the Pied Flycatcher breed for the first time two years after they have fledged (Nyholm 1986), we would expect positive relationships between the number of fledglings in year x and the number of initiated clutches in year x+2. The only significant correlation was that for Lierne (Table 2). The numbers of initiated clutches in Lierne and Ammarnäs were positively related to the number of produced young in the source population of Hemsedal two years earlier (Table 2).

Trends in population size

The trend through the years (t) of the number of initiated clutches (y) in the Hemsedal population was best represented by a quadratic model ($F_{2,17} = 13.59$, $y = 85.94 - 6.10 t + 0.25 t^2$, $r^2 = 0.62$). The model indicates a positive trend in numbers of clutches initiated during the second half of the study (Fig. 6A). The number of successful clutches showed a cubic pattern over the years ($F_{3,16} = 12.06$, $y = 87.49 - 10.70 t + 0.86 t^2 - 0.02 t^3$, $r^2 = 0.69$), indicating an improvement during the last decade, but also a slight backlash during the last years (Fig. 6B).

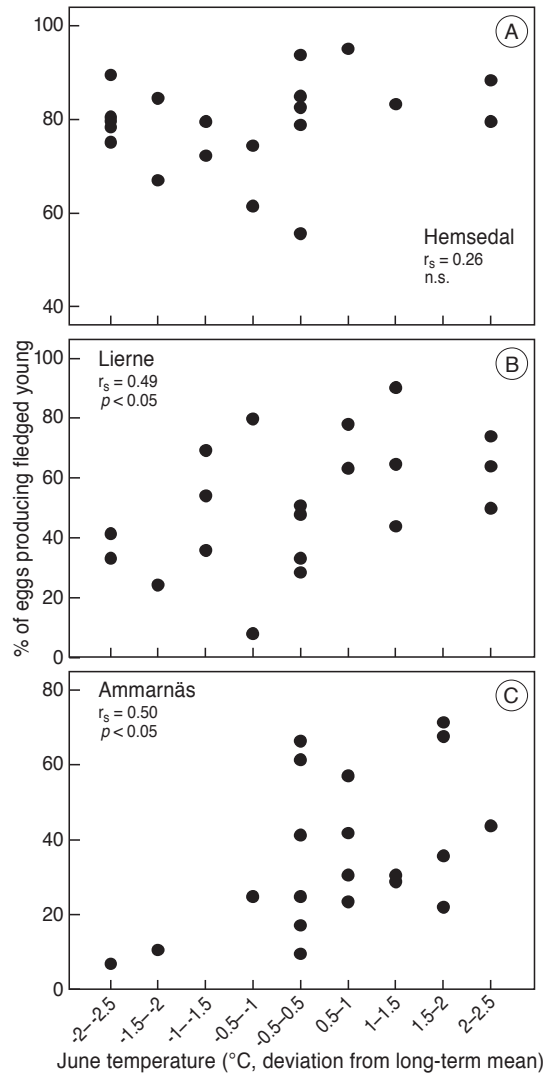The best fit for the number of initiated clutches in the Lierne population was obtained by a cubic

Figure 5. Relationship between breeding success and mean June temperatures in (A) Hemsedal, (B) Lierne and (C) Ammarnäs. Temperatures are deviations from the normal June temperature at the nearest meteorological station.

model ($F_{3,16} = 40.51$, $y = 19.66 + 1.55 t - 1.39 t^2 + 0.01 t^3$, $r^2 = 0.88$). This model suggests an improvement of the local population size during the last years (Fig. 6C). In contrast, the number of successful clutches was best represented by a lin-

Table 2. Relationships between the number of fledged young in each of the study areas and the number of initiated clutches in the next (x+1) and the following year (x+2).

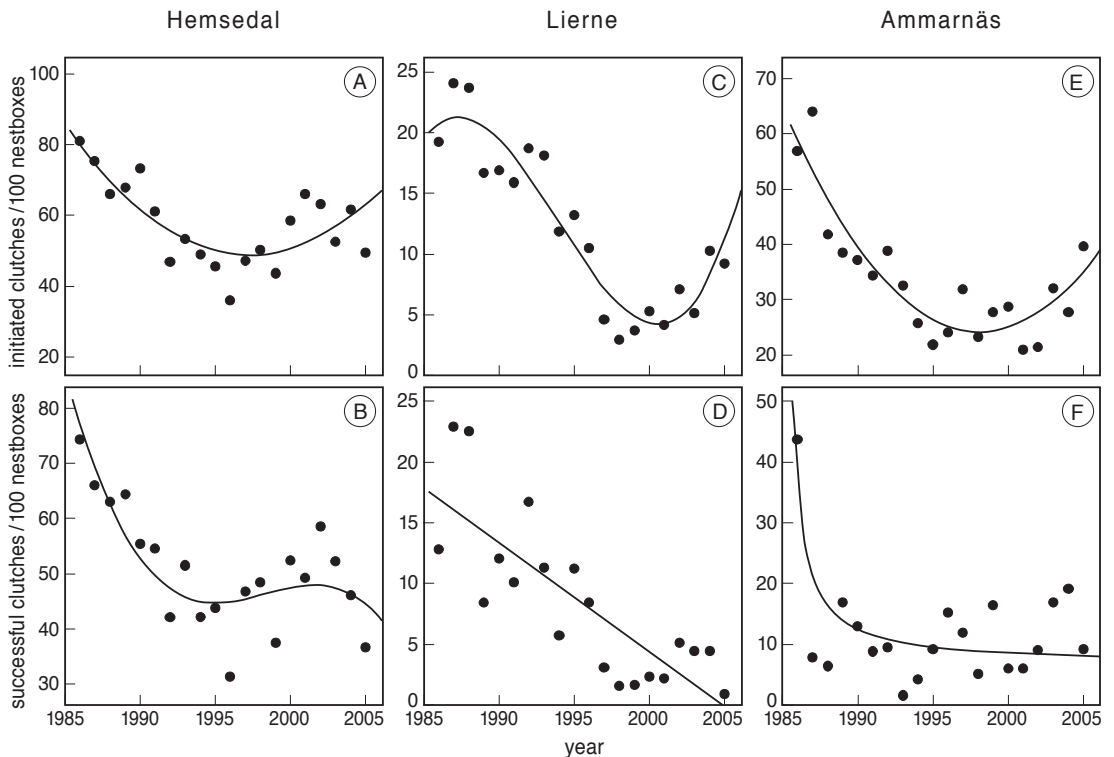| | Number of fledglings year x | | | | | |
| | Hemsedal | | Lierne | | Ammarnäs | |
	r_s	P	r_s	P	r_s	P
Number of initiated clutches year x+1 ($n = 19$)						
Hemsedal	0.58	0.009	0.22	ns	0.21	ns
Lierne	0.22	ns	0.78	<0.001	0.05	ns
Ammarnäs	0.18	ns	0.65	0.002	0.44	ns
Number of initiated clutches year x+2 ($n = 18$)						
Hemsedal	0.43	ns	0.09	ns	0.13	ns
Lierne	0.50	0.033	0.64	0.004	–0.02	ns
Ammarnäs	0.45	ns	0.51	0.029	0.34	ns

Figure 6. Trends for total number of initiated and successful clutches in (A-B) Hemsedal, (C-D) Lierne and (E-F) Ammarnäs during the period 1986–2005. Parameters are expressed as numbers per 100 available nestboxes. See text for further explanation.

ear model ($F_{1,18}$ = 32.85, y = 17.74 – 0.90 t, r^2 = 0.65), implying a continuous negative trend (Fig. 6D).

The numbers of initiated clutches in Ammarnäs was best represented by a quadratic model ($F_{2,17}$ = 35.86, y = 64.51 – 6.15 t + 0.23 t^2, r^2 = 0.81), and also suggested a lately improvement (Fig. 6E). However, the best fit for the numbers of successful clutches followed an inverse model, which implied numbers to stabilise ($F_{1,18}$ = 16.11, y = 6.85 + 27.45/t, r^2 = 0.47; Fig. 6F).

Relationships with the Scandinavian population
The annual production in the study populations was correlated with the migration index in the subsequent autumn (Fig. 7), although the strength of the relationships varied among the populations. In the Hemsedal population the number of successful clutches was significantly correlated with the index (Fig. 7A), and so was the number of fledged young (r = 0.59, P < 0.01). Also in the Lierne population the numbers of successful clutches were strongly correlated with the autumn index (Fig. 7B), as were the numbers of fledged young (r = 0.79, P < 0.01). In the Ammarnäs population neither measure of breeding success was significantly correlated with the autumn index (r = 0.18 and 0.17, respectively), which we attribute to the high predation rate in this area.

The numbers of initiated clutches in the three study areas were well correlated with the autumn migration index during the previous autumn. Correlation was strongest for the Ammarnäs population (Fig. 7C) but also significant for Lierne and Hemsedal (r = 0.53 and 0.54, respectively, n = 19, P < 0.05).

DISCUSSION

Source–sink
According to Järvinen (1983) the theoretical estimate for the critical value for self-maintenance of northern Pied Flycatcher populations is an annual mean number of 4.4 produced fledglings. Otherwise the areas have to be considered as sink habi-
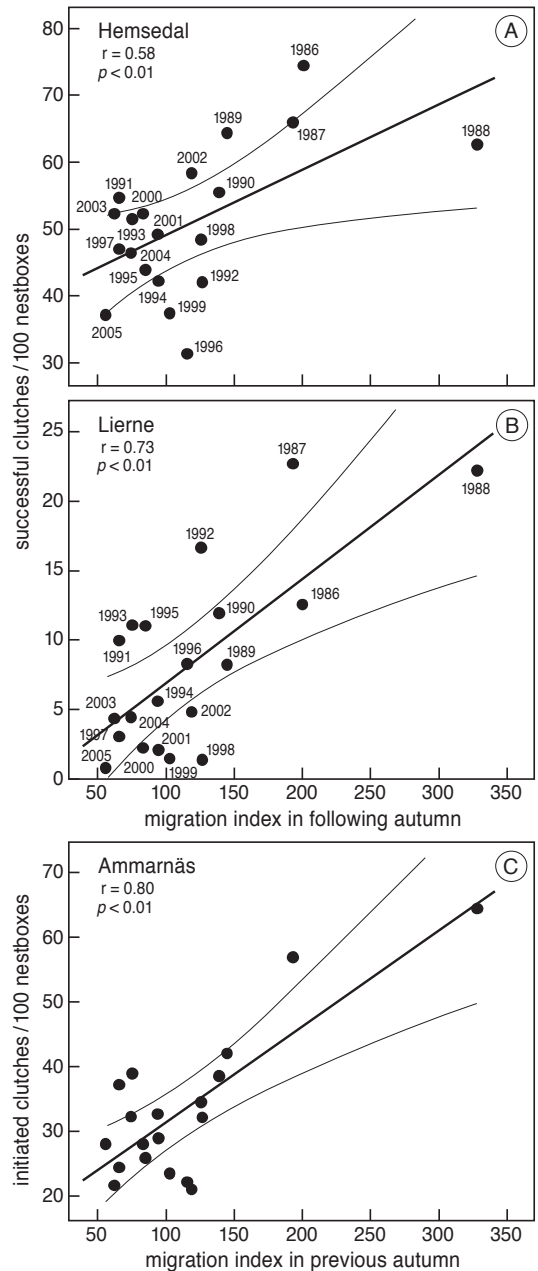
Figure 7. Relationship (with 99% confidence intervals) between total number of successful clutches in (A) Hemsedal and (B) Lierne and the migration index in the following autumn (see text). (C) Relationship between the number of initiated clutches in Ammarnäs and the autumn migration index in the previous autumn.

tats, which implies that they are dependent on annual immigration of surplus individuals from surrounding source populations. Our observations suggest therefore that both Lierne and Ammarnäs are sink habitats. Hemsedal, in contrast, has an annual production that in most years meets the criterion for being a source area. The dichotomy between the three study sites is also demonstrated by the difference in the coefficients of variation of demographic parameters, which are larger for the two sink habitats than for the source habitat. Likewise, numbers in Lierne and Ammarnäs were synchronised over the years, while fluctuations in Hemsedal were not in phase.

The positive correlations between the number of successful clutches in Hemsedal in one year and the number of initiated clutches two years later in Lierne and Ammarnäs indicate also a classical source–sink situation. We do not suggest however that Hemsedal is the actual source for the other study sites, but we assume that the area is representative for other source populations in the Fennoscandian subalpine zone. The time-lag of two years is because the majority of Pied Flycatchers were found to breed for the first time two years after they fledge (Nyholm 1986). As a conclusion, we found indications that confirm the sink status of the Lierne and Ammarnäs populations on the one hand, and the source status of the Hemsedal population on the other.

Weather influence

Several Fennoscandian studies of the Pied Flycatcher showed a negative trend for local populations since the 1970s (Enemar *et al.* 1984, Virolainen 1984, Solonen 1986, Petersen & Brøgger-Jensen 1992, Thingstad & Fjeldheim 1999, Nyholm unpubl. data). The cause of these reductions might be related to weather conditions during the migration periods or in the wintering areas in western Africa (Boehning-Gaese & Bauer 1996, Foppen & Reijnen 1996). The reduction of the British Sedge Warbler *Acrocephalus schoenobaenus* population by about two-third between the mid 1960s and mid 1980s coincided, for instance, with changes in rainfall in the African winter quarters (Peach *et al.*

1991). The Sahel rainfall is characterized by year to year and decadal time scale variability, but with an extended wet period in 1950–69, and an extended dry period in 1970–1997. Therefore, the prolonged drop in the overall population of the Pied Flycatcher was most likely associated with unfavourable conditions on their wintering areas during this period. Our observations suggest an increasing Pied Flycatcher population in recent years. This is in agreement with the reported increase since 1999 of the Whitethroat *Sylvia communis* population in Britain and Ireland (Clark *et al.* 2002).

Recent climate change at the breeding grounds has been mentioned as a possible explanation for the declining populations within West-European habitats, as the flycatchers might have been unable to adjust their breeding to coincide with an earlier peak in abundance of their insect food. Therefore, the timing of spring arrival might constrain the breeding success in the centre of the breeding range (Both 2002, Coppack & Both 2002, Both *et al.* 2004). In the peripheral, subalpine habitats in Fennoscandia the arrival time seems to be of less importance, as the local breeding populations have to adjust their time of egg-laying to the prevailing snow and weather conditions at the breeding ground during spring (Thingstad 1997). During our study period the onset of spring has occurred only slightly earlier in Lierne and Hemsedal, and there was no change discernable in Ammarnäs (http://projects.itek.norut.no/phenology/no/). This agrees with our contention that June temperatures in our study areas have not changed during the study. Moreover, during the last two decades there has been no evidence of any trend in arrival date of spring migrants in northern Norway (Barrett 2002). Therefore, climatic changes in Europe are unlikely to be responsible for any of the revealed population trends within our study populations, regardless their source or sink status, during the last 20 years.

Border populations as indicators

Many local European populations of Pied Flycatcher have shown negative trends since the 1970s; in

central West Europe particularly within rich deciduous forest habitats (Both 2002, Coppack & Both 2002). In contrast, east-European populations seem to be more stable (BirdLife International 2004), and in various less productive coniferous forest habitats in West and Middle Europe the size of populations has increased during the last decades (Cramp & Perrins 1993, Winkel 1993, Winkel & Winkel 1998). Likewise, in Finland numbers have increased from the 1990s onwards (Svensson *et al.* 1999). The trend measured over the European population in the period 1980–2003 was a decline of 24% (European Bird Census Council, www.ebcc.info).

Regardless of the reasons for the observed population reductions since the start of our monitoring project, the models for the numbers of initiated clutches suggested a recovery since the late 1990s, in particular for the source population in Hemsedal. The numbers of successful clutches have partly recovered in Hemsedal (with a slight setback in the two last years), but are still at a low level in the two sink populations (Lierne and Ammarnäs).

The relationships between the autumn migration index and numbers of successful clutches were significant for the Lierne and Hemsedal populations, while the Ammarnäs population failed to show any correlation probably due to severe and variable predation of nests. Interestingly, the numbers of initiated clutches in all our study areas were well correlated with the autumn migration index in the previous autumn.

The peak in numbers in 1988 and the low values around 2000 coincided in the two sink populations and in the autumn migration index. This pattern was not visible in the source population of Hemsedal, which in this respect resembled the Swedish breeding population (Edvardsen *et al.* 2004). It seems therefore that variation in the Fennoscandian population as a whole is most clearly visible in marginally located sink habitats in the subalpine zone. In periods of shrinking populations they might therefore be functioning as an early warning indicator for the situation of the overall population.

REFERENCES

Barret R.T. 2002. The phenology of spring bird migration to north Norway. Bird Study 49: 270–277.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. Cambridge, UK.

Boehning-Gaese K. & Bauer H.G. 1996. Changes in species abundance, distribution, and diversity in a central European bird community. Conserv. Biol. 10: 175–187.

Both C. 2002. Nemen Bonte Vliegenvangers *Ficedula hypoleuca* af door klimaatsverandering? Limosa 75: 73–78.

Both C., Artemyev A.V., Blaauw B., Cowie R.J., Dekhuijzen A.J., Eeva T., Enemar A., Gustafsson L., Ivankina E.V., Järvinen A., Metcalfe N.B., Nyholm N.E.I., Potti J., Ravussin P.-A., Sanz J.J., Silverin B., Slater F.M., Sokolov L.V., Török J., Winkel W., Wright J., Zang H. & Visser M.E. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc. R. Soc. Lond. B 271: 1657–1662.

Clark J.A., Balmer D.E., Adams S.Y., Grantham M.J., Blackburn J.R., Robinson R.A., Wernham C.V., Griffin B.M. & Milne L.J. 2002. Bird ringing in Britain and Ireland in 2001. Ring. Migrat. 21: 80–143.

Coppack T. & Both C. 2002. Predicting life-cycle adaption of migratory birds to global climate change. Ardea 90: 369–378.

Cramp S. & Perrins C. (eds) 1993. The birds of western Palearctic. Vol. VII. OUP, Oxford.

Edvardsen E., Røer J.E., Solvang T.E., Rafoss T. & Klaveness G. 2004. Bestandsovervåkning ved standardisert fangst og ringmerking ved fuglestasjonene. Norsk Ornitologisk Forening Rap. 2004-3: 1–29.

Enemar A., Nilsson L. & Sjöstrand B. 1984. The composition and dynamics of the passerine bird community in a sub-alpine birch forest, Swedish Lapland. A 20-year study. Ann. Zool. Fennici 21: 231–338.

Enemar A., Sjöstrand B., Andersson G., Von-Proschwitz T. 2004. The 37-year dynamics of a subalpine passerine bird community, with special emphasis on the influence of environmental temperature and *Epirrita*

autumnata cycles. Ornis Svecica 14: 63–106. (In Swedish with English Summary)

Foppen R. & Reijnen R. 1996. The willow warbler *Phylloscopus trochilus* in trouble: Africa involved? Limosa 69: 51–56.

Gaona P., Ferreras P. & Delibes M. 1998. Dynamics and viability of the endangered Iberian Lynx (*Lynx pardinus*). Ecol. Monogr. 68: 349–370.

García J.T. & Arroyo B.E. 2001. Effect of abiotic factors on reproduction in centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. Ecography 24: 393–402.

Haftorn S. 1957. Recent changes in the avifauna of North Norway, results from a journey in 1955. Kgl. Norske Vidensk. Selsk. Forh. 26: 76–82. (In Norwegian with English summary)

Haftorn S. 1971. Norges fugler. Universitetsforlaget, Oslo.

Hoffmann A.A. & Blows M.W. 1994. Species borders: ecological and evolutionary perspectives. Trends Ecol. Evol. 9: 223–227.

Howe R.W., Davis G.J. & Mosca V. 1991. The demographic significance of "sink" populations. Biol. Conserv. 57: 239–255.

Järvinen A. 1983. Breeding strategies of hole-nesting passerines in northern Lapland. Ann. Zool. Fennici 20: 129–149.

Järvinen A. & Väisänen R.A. 1984. Reproduction of Pied Flycatcher (*Ficedula hypoleuca*) in good and bad breeding seasons in northern marginal areas. Auk 101: 439–450.

Lundberg A, 1997. *Ficedula hypoleuca*. Pied Flycatcher. In: Hagemeijer E.J.M. & Blair M.J. (eds). The EBCC Atlas of European breeding birds: Their distribution and abundance: 621. T. & A.D. Poyser, London.

Lundberg, A. & Alatalo, R.V. 1992. The Pied Flycatcher. T. & A.D. Poyser, London

Mehlman, D.W. 1997. Change in avian abundance across the geographic range in response to environmental change. Ecol. Appl. 7: 614–624.

Murphy M.T. 2001. Source-sink dynamics of a declining eastern kingbird population and value of sink habitats. Conserv. Biol. 15: 737–748.

Nyholm N.E.I. 1986. Birth area fidelity and age at first breeding in a northern population of Pied Flycatcher *Ficedula hypoleuca*. Ornis Scand. 17: 249–252.

Petersen, B.S. & Brøgger-Jensen, S. 1992. The populations of common Danish woodland birds 1976–1990. Dansk Orn. For. Tidsskr. 86: 137–154.

Peach W., Baillie S. & Underhill L. 1991. Survival of British Sedge Warbler *Acrocephalus schoenobaenus* in relation to West African rainfall. Ibis 133: 300–305.

Sanz J.J. 1995. Environmental restrictions on reproduction in the pied flycatcher *Ficedula hypoleuca*. Ardea 83: 421–430.

Sanz J.J. 2003. Large-scale effect of climatic change on breeding parameters of pied flycatcher in Western Europe. Ecography 26: 45–50.

Sillett T.S., Holmes R.T. & Sherry T.W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288: 2040–2042.

Solonen T. 1986. Stability of a bird community in southern Finland. Ornis Scand. 17: 106–116.

Svensson S., Svensson M. & Tjernberg M. 1999. Svensk fågelatlas. Vår Fuglefauna, Suppl. 31. Stockholm.

Sætre G.-P., Borge T., Lindell J., Moum T., Primmer C.R., Sheldon B.C., Haavie J., Johnsen A. & Ellegren H. 2001. Speciation, introgressive hybridization and nonlinear rate of molecular evolution in flycatchers. Mol. Ecol. 10: 737–749.

Sæther B.E. 2000. Weather ruins winter vacations. Science 288: 1975–1976.

Thingstad P.G. 1997. Annual and local reproductive variations of a pied flycatcher *Ficedula hypoleuca* population near a subalpine lake in central Norway. Ornis Fenn. 74: 39–49.

Thingstad P.G. & Fjeldheim B. 1999. Can a 12-year study of the pied flycatcher *Ficedula hypoleuca* reveal the breeding population dynamics? Vogelwelt 120, Suppl.: 355–360.

Virolainen M. 1984. Breeding biology of the pied flycatcher in relation to population density. Ann. Zool. Fennici 21: 187–197.

Winkel W. 1993. Langfristige Bestandsdynamik von Höhlenbrütern (*Parus, Sitta, Phoenicurus, Ficedula, Jynx*) im Braunschweiger Raum. Jber. Inst. Vogelforsch. 1: 20–21.

Winkel W. & Winkel D. 1998. Bestandszunahme des Trauerschnäppers (*Ficedula hypoleuca*) am Westrand seines mitteleuropäischen Verbreitungsareals. Vogelwarte 39: 222–224.

SAMENVATTING

Tegenwoordig is de Bonte Vliegenvanger *Ficedula hypoleuca* een algemene broedvogel in Fenno-Scandinavië, de Baltische staten en (Wit-)Rusland. De expansie naar het noorden is waarschijnlijk een recente ontwikkeling. De meest noordelijke gebieden zijn pas na 1800 bereikt. De perifere populaties in de subalpine bossen van Fenno-Scandinavië laten sinds de jaren 1970 een achteruitgang zien, na een snelle groei gedurende de voorafgaande decennia. Recent is er een herstel waargenomen en nemen de aantallen weer toe. De auteurs verwachtten dat de populaties in de subalpine bossen extra gevoelig zijn voor de veranderingen waaraan de gehele Fenno-Scandinavische populatie onderhevig is en daarom goede

indicatoren zijn voor het welbevinden van die populatie. Het onderhavige onderzoek beschrijft het broedsucces en de populatiefluctuaties tussen 1986 en 2005 in drie bosgebieden in Scandinavië: Hemsedal in Zuid-Noorwegen, Lierne in Midden-Noorwegen en Ammarnäs in Noord-Zweden. Deze bossen liggen aan de grens van het verspreidingsgebied van Bonte Vliegenvangers, maar verschillen onderling in kwaliteit. De demografische ontwikkelingen van de noordelijke broedpopulaties in Lierne en Ammarnäs zijn karakteristiek voor zogenaamde 'sink' populaties (jaarlijkse aanwas onvoldoende om de populatie in stand te houden). De meest zuidelijke populatie, in Hemsedal, is een 'source' populatie (overmaat aan jongen). 'Sinks' kunnen blijven bestaan dankzij immigratie uit 'sources'. De achteruitgang in aantallen broedvogels gedurende de laatste dertig jaar was het meest prominent in Lierne en Ammarnäs. De achteruitgang werd waarschijnlijk veroorzaakt door de weersomstandigheden in de overwinteringsgebieden in West-Afrika. Er werden geen aanwijzing gevonden voor een klimaatsverandering in het broedgebied. De jaarlijkse fluctuaties in broedsucces correleerden echter wel met de jaarlijkse variatie van de temperatuur in de maand juni. Momenteel groeien alle drie de populaties weer. De toename is het meest duidelijk in het zuidelijke Hemsedal; in Lierne en Ammarnäs zijn de veranderingen veel trager en van jongere datum. Om de verandering in de broedgebieden te relateren aan populatietrends in de hele regio, gebruikten de auteurs najaarsgegevens van Zuid-Scandinavische ringstations (Falsterbo, Lista and Jomfruland). De ringactiviteiten in de drie stations zijn min of meer gestandaardiseerd, zodat het aantal geringde vogels in het najaar kon worden gebruikt als index voor het aantal doortrekkers. Het aantal legsels in de 'sink' populaties in Lierne en Ammarnäs vertoonde een positieve trend met de index in de herfst erna. Voor Lierne en Hemsedal vonden de auteurs ook een significante correlatie tussen het aantal succesvolle legsels en de najaarsindex. Voor Ammarnäs was er geen correlatie tussen de laatste twee parameters, vermoedelijk vanwege de hoge predatiedruk. De auteurs concluderen dat de drie bestudeerde perifere populaties samen een goede indicatie geven voor populatieveranderingen in heel Scandinavië.   (YIV)