

Breeding-site fidelity and dispersal in isolated populations of three migratory passerines

Dmitry Shitikov, Svetlana Fedotova, Victoria Gagieva, Darya Fedchuk, Elena Dubkova & Tatiana Vaytina

D.A. Shitikov, The research group of Avian population ecology, Zoology and Ecology Department, Moscow Pedagogical State University, Moscow, 129278, Russia. E-mail dash.mpgu@gmail.com

S.E. Fedotova, The research group of Avian population ecology, Zoology and Ecology Department, Moscow Pedagogical State University, Moscow, 129278, Russia

V.A. Gagieva, The research group of Avian population ecology, Zoology and Ecology Department, Moscow Pedagogical State University, Moscow, 129278, Russia

D.V. Fedchuk, Bioecology Department, International Independent Ecological and Politological University, Moscow, Russia

E.V. Dubkova, The research group of Avian population ecology, Zoology and Ecology Department, Moscow Pedagogical State University, Moscow, 129278, Russia

T.M. Vaytina, The research group of Avian population ecology, Zoology and Ecology Department, Moscow Pedagogical State University, Moscow, 129278, Russia

Received 17 January 2011, accepted 9 June 2011

Living in an isolated patch may increase, for example, the extinction risk of a local population, but such risks may be mitigated by natal and breeding dispersal. We therefore analyzed five years of Russian banding data on Booted Warbler, Whinchat and Yellow Wagtail (*Hippolais caligata*, *Saxicola rubetra* and *Motacilla flava*, respectively), within a 20-ha abandoned meadow, isolated from similar habitat by vast areas of woodland. We individually banded 203 Booted Warblers, 193 Whinchats and 83 Yellow Wagtails. During the years following banding, four males of Booted Warbler (2.0%), one male of Whinchat (0.4%) and 11 Yellow Wagtails (13.3%; 7 males and 4 females) returned to the study meadow. The apparent survival rate of the Yellow Wagtail was significantly higher than that of the Whinchat and Booted Warbler. For the Yellow Wagtail, the yearly numbers of recoveries varied considerably, and were linked with previous-year breeding success. Successful years were usually followed by returns to the same site next year. Moreover, recoveries of individuals that were born at the study site during the preceding years were extremely scarce (two out of a total of 258 banded nestlings). These findings suggest two important aspects: (1) species-specific returning rates and annual fluctuation in these are largely defined by mortality and reproductive success during the previous year, and (2) local populations of all three species are apparently mostly formed by immigrants, implying that local nestling production may not contribute significantly to the local population. The negative consequences of living in isolated patches of habitat may be mitigated by natal and breeding dispersal.



1. Introduction

Individuals of many migratory bird species tend to return to the same location each year for breeding. This breeding-site fidelity and natal philopatry are major determinants of the geographic distribution and population structure of avian populations (Greenwood 1980, Greenwood & Harvey 1982). The rates of site fidelity and philopatry influence population dynamics and demography (Brown & Kodric-Brown 1977, Wheelwright & Mauck 1998) and may play a critical role in source-sink dynamics and the maintenance and demographic rescue of small or isolated populations (Lande & Barrowclough 1987, Payne 1991, Sedgwick 2004).

Previous studies have identified numerous correlates of site fidelity, the most influential being variation in reproductive success in the previous season (Bollinger & Gavin 1989, Weatherhead & Boak 1986, Haas 1998, Hoover 2003, Newton 2003, Sedgwick 2004). Birds may also use habitat or site quality as a criterion in deciding whether to return (Greenwood 1980, Lanyon & Thompson 1986, Bollinger & Gavin 1989, Holmes *et al.* 1996). Site fidelity often differs between sexes and ages, being usually greater in males than in female birds and in older rather than in younger individuals (Greenwood 1980, Holmes *et al.* 1996, Clarke *et al.* 1997).

One of the factors that influence the site fidelity and natal philopatry of passerines can be the degree of isolation from other local populations. Significant increase in the rate of site fidelity in isolated populations, compared to known averages, has been commonly documented (Wittenberger 1978, Mewald & King 1985, Lanyon & Thompson 1986, King & Mewald 1987, Roth & Johnson 1993). Annual return rates of adult passerines may reach 60–80% at small isolated patches of habitat (King & Mewald 1987, Roth & Johnson 1993). Consequently, within small, isolated areas breeding dispersal may be poorly if at all expressed, and all surviving individuals may return to the preceding nesting site. On the other hand, the site-fidelity rate of island populations could be minor, in which case these islands become populated by birds of more random origin (Lapshin 2001).

In passerines, natal philopatry is often lower than the site fidelity of adults, especially in migra-

tory species (Weatherhead & Forbes 1994), and high natal philopatry is mostly found in isolated populations (Lawn 1982, Zubcovsky *et al.* 1989, Sokolov 1991, Wheelwright & Mauck 1998, Förschler *et al.* 2010). The high natal philopatry at isolated areas can sometimes be explained by the spatial limitation of post-fledging dispersal: young individuals imprint the nearest surroundings of their nests and return to that place in subsequent years (Zubcovsky *et al.* 1989, Sokolov 1991, Förschler *et al.* 2010).

Differences in site fidelity and natal philopatry among local populations of a given species can be described with the source-sink concept (Pulliam 1988). Migratory birds may be characterized as having source-sink population dynamics in which some individuals nest in “source” habitats where offspring production exceeds mortality, and others are forced to nest in “sink” habitats where reproduction does not compensate for adult and juvenile mortality (Donovan *et al.* 1995). Sites with high rates of nest predation would serve as population sinks and should be avoided by returning birds (Donovan *et al.* 1995, Hoover 2003).

Here we present observations on site fidelity and natal philopatry in three passerine species within an isolated patch of suitable habitat in the European North of Russia. The main aims of this study were (1) to estimate the local survival rates of the young and adult individuals and to determine the impact of the reproductive success on these rates; (2) to define the scope of the natal and breeding dispersal of the model species; and (3) to identify the role of the local birds and immigrants in the formation of the local populations.

2. Material and methods

2.1. Study site

The research was carried out in Russian North National Park (hereafter referred to as park), located in the north-west of the European part of Russia in Kirillov district of Vologda region. The district is mostly covered with woodlands. Agricultural lands consist of fields of spring crops and flax (*Linnum usitatissimum*) and meadows, and they cover less than 10% of the area. These lands are mostly represented by 10–200 ha patches divided

by forested land. Our study plot was a 20-ha humid grass-forb meadow overgrowing with osier bushes (*Salix sp.*) situated in the north-western part of the National park near the Chistii Dor village (60°09' N; 38°22' E). On one side the study plot borders coniferous and small-leaved forest, and on the other side it is surrounded by fields of spring crops and flax with total area of about 160 ha. Within 0.1–1 km from the study plot, grassland occurs on only small isolated patches, with a total area of 4–5 ha. The nearest meadows of comparable size (20–30 ha) were situated 5–7 km away from the study plot, and larger meadows (>50 ha) were over 10 km away and always separated by contiguous woodlands.

2.2. Study species

We studied three species from the order Passeriformes: Booted Warbler (*Hippolais caligata*), Whinchat (*Saxicola rubetra*) and Yellow Wagtail (*Motacilla flava*). These model species are widespread in the European North of Russia, where they inhabit various types of grassland, from small highly-fragmented patches among forested areas to extensive floodplain meadows (Butyev & Ezhova 1987, Shitikov 2000, Butyev *et al.* 2007, Shitikov & Fedchuk 2008). All these three species are long-range migrants: Whinchat and Yellow Wagtail winter in Africa south of Sahara, and Booted Warbler winters in India (Cramp 1988, 1992).

Whinchat shows a high site-fidelity rate: at different parts of its geographical range 10–48% of adults return to the plot of their previous year's breeding, although females tend to return to the same plot less frequently (Schmidt & Hantge 1954, Bastian 1992, Müller *et al.* 2005, Shitikov & Fedchuk 2008). Return rates of young birds are considerably lower: only from 1–2% to 11–17% of second-year individuals return to the place of birth (Bastian 1992, Müller *et al.* 2005). Data on site fidelity in the Yellow Wagtail are scarce. On Helgoland, Germany, 21% of banded birds returned after one year, and 8% of the original cohort returned after two years (Drost 1948); females returned in nearly equal proportions to males. In western Alaska, 52% of Eastern Yellow Wagtail (*Motacilla flava tchutchensis*) males, banded in

Table 1. The numbers of territorial pairs, banded males (including returning individuals the following year after banding) and banded females of the three model species (pairs/males/females).

Year	Booted Warbler	Whinchat	Yellow Wagtail
2005	22*/15/17	16/10/13	7/1/2
2006	19/14/12	18/11/10	5/5/5
2007	30/24/21	19/16/13	7/5/4
2008	28/16/7	9/6/3	7/6/2
2009	14/1/0	4/0/0	1/1/1

* 17 territorial pairs and 5 single males

nests, returned, but none of the controlled females were returning (Renner & McCaffery 2008). In that study, only one of the 70 banded nestlings (1.4%) returned to the same site the following year. Data on site fidelity in the Booted Warbler were not available.

2.3. Data collection

We caught Booted Warblers and Whinchats between 2005 and 2009, and Yellow Wagtails between 2005 and 2010. The field work was carried out in three periods, which allowed us to determine the size of the nesting population of a given species, and to band more adults and nestlings (Table 1). The first period was done during a period of 1–2 days between the end of May and the beginning of June (bird counts and nest searches), the second period was 5–7 days in mid-June, and the third period took 1–3 days in the beginning of July. Capturing and banding were conducted in the mid-June period, and some birds were banded in July. Occasionally the field work could not be completed within the time schedule, and in these cases the study plot was revisited within a few days from the end of a given period.

Bird counts were conducted daily during each of the three periods by mapping the male territories within the 20-ha study meadow (Wiens 1969). Territory locations and numbers were confirmed by comparing the count data with data on detected nests. To detect banded birds, we conducted similar censuses at an isolated 4-ha “control” meadow 500 m from the perimeter of the 20-ha study meadow and at another small meadow near Chistii

Dor village. These censuses were conducted twice per season. We were unable to detect the study species from agricultural land (spring crops and flax).

Adult birds were captured with mist nets, and spring traps were used at nests. Most of the adults were captured in mid-June, but additional trapping took place in early July. We set 3–10 mist nets, with their location changed every 1–2 days, within the 20-ha study meadow. All captured birds were banded with standard metal rings and individual combinations of color rings. Nestlings of 5–8 days of age were banded in nests using a standard numbered metal ring and one color ring. All nestlings of a given year were banded using the same color. The banding was most intense between 2005 and 2007. In 2009 we only monitored the previously-banded Booted Warblers and Whinchats. The banding of Yellow Wagtails was continued up to 2009, and in 2010 we only monitored returns of banded individuals.

During each census, and for each territorial pair, we specifically aimed at detecting and reading color rings in the field. Whenever we found territorial, non-ringed birds, we set mist nets or spring traps on the nest to ring these individuals. Spring traps were used only on nests with nestlings at the age of at least five days, because parents might abandon nests with clutches and younger nestlings as a consequence of a capturing attempt. Adult Booted Warblers were also captured with mist nets set near such nests that had clutches. Each territory with a breeding pair was visited at least five times per season. We also looked for banded individuals at the isolated “control” meadow (see above). We banded annually 50–100% of adults nesting within the 20-ha study meadow; however, this percentage was occasionally lower (Table 1). We determined the age of all adult Whinchat males since 2006 according to the white patterning in the primary coverts (Schmidt & Hantge 1954, Svensson 1984, Jenni & Winkler, 2004).

Simultaneously with the above-explained study, additional background data were collected at the Topornya ringing station (59°76' N, 38°22' E). This station is located at a 5-km² area of meadows and abandoned agricultural land around Topornya village in the southern part of the Russian North National Park (Shitikov & Fedchuk 2008, Shitikov *et al.* 2008). At this area, birds were banded

and monitored within the total territory of 3 km². These data allowed us to examine possible long-range dispersal between Chistii Dor and the meadow plots: the distance between these is 43 km.

2.4. Data analysis

We estimated adult apparent survival (φ) and recapture (p) rates using Cormack-Jolly-Seber models (Lebreton *et al.* 1992) using MARK 6.0 software (McClintock & White 2010). We used the implementation of RELEASE available in MARK to conduct goodness-of-fit tests on the data (all $p > 0.05$) and to compare apparent survival rates of the model species. A set of 16 models alternating constant, time (t) and sex (g) effect for φ and p were developed for Yellow Wagtail. The general model was (i) $\varphi(g^*t)p(g^*t) - g$. Constant models were (ii) $\varphi(g)p(g^*t)$; (iii) $\varphi(t)p(g^*t)$; (iv) $\varphi(.)p(g^*t)$; (v) $\varphi(g^*t)p(t)$; (vi) $\varphi(g)p(t)$; (vii) $\varphi(t)p(t)$; (viii) $\varphi(.)p(t)$; (ix) $\varphi(g^*t)p(g)$; (x) $\varphi(g)p(g)$; (xi) $\varphi(t)p(g)$; (xii) $\varphi(.)p(g)$; (xiii) $\varphi(g^*t)p(.)$; (xiv) $\varphi(g)p(.)$; (xv) $\varphi(t)p(.)$ and (xvi) $\varphi(.)p(.)$.

As we detected no returns for females of Whinchat and Booted Warbler, apparent survival and recapture rates for these species were calculated only for males. The Akaike Information Criterion corrected for small-sample bias (AIC_c) was used to rank the fit of each model to the data (Anderson & Burnham 2002). The model with the lowest AIC_c and greatest weighting was taken as the best representation of the data. Models were run using the logit link function.

Every nest location was determined using a Geographic Positioning System (GPS). All positions were transferred to digital maps using Mapinfo 9.0 (Pitney Bowes MapInfo Corp. 2007) software. We defined the breeding dispersal as being the distance between two nests of the same bird in two consecutive years. In most cases the range of breeding dispersal was defined by size and shape of the study plot (850 × 500 m). Our data did not allow us to calculate the daily survival rates (Mayfield 1975), which is why the reproductive success was estimated as being the proportion of successful nests by the total number of nests with a known fate. The nest was considered successful if at least one chick fledged and entered the juvenile stage.

Table 2. Apparent survival rates (ϕ ; mean \pm SE) of the model species. In 2009 only Yellow Wagtails were banded.

Year	Whinchat, males	Booted Warbler, males	Yellow Wagtail, males	Yellow Wagtail, females
2005	0	0.27 \pm 0.11	1.00 \pm 0.00	0.5 \pm 0.35
2006	0.08 \pm 0.07	0.07 \pm 0.06	0.20 \pm 0.17	0.4 \pm 0.22
2007	0	0.04 \pm 0.04	1.00 \pm 0.00	0.5 \pm 0.35
2008	0	0	0	0
2009	–	–	1.00 \pm 0.0	0

3. Results

During the 2005–2010 study, we found a total of 48 nests of Booted Warbler, 34 of Whinchat and 17 of Yellow Wagtail within the 20-ha meadow patch. In total we banded 203 Booted Warblers (64 males, 57 females and 82 nestlings), 193 Whinchats (42 males, 39 females, 112 nestlings), and 83 Yellow Wagtails (11 males, 8 females, 64 nestlings) within the 20-ha meadow. Moreover, outside the 20-ha meadow, i.e., in nearby “control” meadows (see Material and methods), we detected yearly 4–10 pairs of Booted Warblers, 5–9 pairs of Whinchats and 1–2 pairs of Yellow Wagtails. According to a comparison between the 20-ha study meadow and these “control” meadows, the numbers of all the three species remained stable during 2005–2007 but in 2008 Whinchat started to decline, Booted Warbler decreased by two-fold between 2008 and 2009, and Yellow Wagtail was nearly absent since 2009 (Table 1).

3.1. Breeding-site fidelity and breeding dispersal

The site fidelity of the Whinchats at our study plot was low; we registered only one return of a Whinchat in the banded previous year. This territorial male, captured with a mist net on 6 June 2006 at the age of at least three calendar years, nested 143 m from the point of capture the following year. We also registered one event of long-range breeding dispersal for this species: an adult male, captured in the nest in 2007 at the age of at least three calendar years, was spotted nesting on an abandoned pasture in the southern part of the park in 2009. The distance between its nests in

2007 and 2009 was 43 km 150 m. In 2008 we did not register this individual at our research stations.

Of the 64 banded Booted Warbler adult males, four returned to the study meadow during years following banding, while none of the 57 banded adult females returned. Three males nested in the study meadow only the following year after the banding year, but one nested for three consecutive years there. In our data, the breeding dispersal of Booted Warbler males was 160 ± 31 m (variation 100–300 m; $n = 6$).

For the Yellow Wagtail, we registered 13 returns of 11 individuals (7 males and 4 females); one male and one female returned for two consecutive years. In some years (2008 in particular) all banded males and half of the banded females returned to the study meadow, while in 2009 none of the Yellow Wagtails banded in 2008 returned. For one pair, the female bred in 2009 but did not return in 2010, while the male was spotted breeding successfully with an unmarked female on a 4-ha patch of abandoned meadow 883 m from its previous year’s nest. This is actually the only case of the nesting of a returning adult outside the study meadow. The breeding dispersal of males was 265 ± 104 m (variation 100–883 m; $n = 7$), and that of females was 82 ± 28 m (25–140 m; $n = 4$). The breeding dispersal of males and females did not differ significantly (Mann-Whitney U test; $Z = 1.6$, $p = 0.11$).

3.2. Apparent survival rate

The most parsimonious model for the Yellow Wagtail included a constant recapture probability (p , 1.0) and apparent survival rate (ϕ) depending on time and sex ($\phi(g^*t)p(\cdot)$). For males of Whin-

chat and Booted Warbler, the most parsimonious model was $\varphi(t)p(\cdot)$. Apparent survival rates, calculated for these models, are shown in Table 2. The apparent survival rate did not significantly differ between the males of Whinchat and Booted Warbler ($\chi^2 = 0.8, p = 0.3$). However, the apparent survival rate was significantly higher for the Yellow Wagtail than for Whinchat ($\chi^2 = 34.52, p < 0.01$) or for Booted Warbler ($\chi^2 = 34.54, p < 0.01$). There were no significant differences in the apparent survival rate of males and females of the Yellow Wagtail ($\chi^2 = 1.91, p = 0.59$).

3.3. Philopatry and natal dispersal

Among all individuals of the three species banded as nestlings at the Chistii Dor station, we registered two individuals in the subsequent years. A Yellow Wagtail male, banded in the nest in 2007, was found breeding in a 4-ha patch of abandoned grassland 500 m from the perimeter of the 20-ha meadow in 2008. Moreover, a Yellow Wagtail female, banded as a nestling in 2008, was seen (breeding not confirmed) in a cluster of 3–4 pairs of Yellow Wagtails 14 km to the east from the place of its birth in 2009. No recoveries of nestlings of Whinchat and Booted Warbler banded at the Chistii Dor station were recorded during the study. Finally, a Booted Warbler male, banded as a nestling in the southern part of the park in 2008, was seen (breeding not confirmed) at the Chistii Dor station, 43 km from the place of birth, in 2009.

3.4. Reproductive success

From the 26 nests of Booted Warbler with known fate, eight (31%) were successful (i.e., produced fledglings), and similarly from the 16 nests of Whinchat five (31%) were successful. The proportion of successful nests of Booted Warbler and Whinchat did not differ markedly ($\chi^2 = 0.01, p = 0.95$). Eleven of the 17 detected Yellow Wagtail nests with known fate (65%) were successful. The reproductive success was significantly higher in Yellow Wagtail than in Booted Warbler ($\chi^2 = 4.8, p = 0.03$) and in Whinchat ($\chi^2 = 3.69, p = 0.05$). The reproductive success of Yellow Wagtail varied considerably from year to year. It was low in 2008

when the nestlings of only one out of seven pairs breeding in the 20-meadow successfully left the nest; another pair had a successful second breeding attempt. In other years reproduction was successful in most of the studied nests.

The probability of returning to a breeding site seems to have been partly related to breeding success at that site. All Yellow Wagtails that had been banded as nestlings and detected as successful breeders the following year, returned to the breeding site the year after a successful attempt. The link between breeding success and returning rate for the Booted Warbler remains unknown, as the nestlings at the age of 8–10 days were still in nests at the time of research completion at the Chistii Dor station. Considering that in the Booted Warbler the average duration of feeding is 10–12 days (Butyev *et al.* 2007), nests with advanced nestlings might have been considered successful. Likewise, we could not determine the breeding success for returning Whinchats, as only one recovery was registered. In this case, a male successfully bred at the Chistii Dor station in 2007 and was relocated at the southern part of the park in 2009, but its nest was not found.

3.5. Age ratio of Whinchat males

Among the captured Whinchat males, those older than two calendar years made up 50–75% of individuals in 2006–2007 (Table 3). In 2008, however, there was a peak in the number of first-breeding (2nd-calendar year) individuals as a result of an overall population decrease in this species that year.

4. Discussion

The site-fidelity rates of the three passerine species inhabiting the small isolated study-meadow patch differed markedly. Yellow Wagtails had high local survival rates for both sexes, exceeding the rates described in literature concerning this species (Drost 1948, Renner & McCaffery 2008). However, the local survival rates of Whinchat and Booted Warbler were considerably lower, and the rate for Whinchat was lower than those reported in other parts of the species' geographical range

Table 3. Trapped Whinchat males according to two age classes.

Year	2nd-cal year	Older
2006	3 (27.3%)	8 (72.7%)
2007	4 (25.0%)	12 (75.0%)
2008	2 (50.0%)	2 (50.0%)
Total	9 (29.0%)	22 (71.0%)

(Schmidt & Hantge 1954, Bastian 1992, Müller *et al.* 2005). Young birds of all the studied species did not return to the place of birth at all, as the philopatry rates on the isolated meadow did not increase (cf. Zubcovsky *et al.* 1989, Wheelwright & Mauck 1998, Förchler *et al.* 2010).

We suggest that the scarcity of returns of young birds can be explained by the absence of barriers for post-fledging dispersal. Some passerine species show within-season shifts of habitat preference that can be related to changes in food supply (Bairlein 1983). For the three species under discussion, local populations can be considered isolated only during the breeding season. Passerine birds breeding in open habitats often perform post-nesting movements through shrubs along country roads and floodplains (Korovin 2004). Such ecological corridors that connect separate isolated patches of habitat may significantly affect post-fledging dispersal (Haas 1995, Beier & Noss 1998). In our case, for example, two unpaved roads with broad verges overgrown with bushes, and willow shrubs at the floodplain of a small river flowing in 500 m from the study meadow could function as such corridors. Indeed, at a verge of one of the roads 14 km to the east from Chistii Dor we registered a female of Yellow Wagtail which had been banded one year before as a nestling at the 20-ha study meadow.

We cannot directly assess the extent of breeding dispersal according to our data, as the models that we applied prevented us from separating true survival rate and dispersal (Lebreton *et al.* 1992). True survival rate of adults among most passerines varies between 30% and 60% (Karr *et al.* 1990, Payevsky *et al.* 1997, Siriwardena *et al.* 1998). So, according to the long-term data of banding in Great Britain, the annual survival of Yellow Wagtail can be estimated to be 53% (Siriwardena *et al.* 1998). For central European populations of

Whinchat, on the other hand, the annual adult survival may be 50–60% (Müller *et al.* 2005). Data concerning true survival of Booted Warbler are lacking, but the rate may be lower than for the other two species because the survival rate in passerines depends on body size (Saether 1989). For the similar-sized Willow Warbler (*Phylloscopus trochilus*), estimates of annual survival rate vary between 30 and 40 percent (Tianen 1983, Baile & Peach 1992, Payevsky *et al.* 1997, Siriwardena *et al.* 1998).

If these rates apply to the Russian population of the three model species, and given the observed local survival rates of birds banded at the Chistii Dor station, it is plausible that the returns of Yellow Wagtail averaged to about 75% of survived adults (70% of females and 80% of males). Hence, in some years all of the surviving birds of both sexes returned to the breeding site of previous year. For the Booted Warbler, 10–80% of males returned in different years, the average being about 30%. The lack of recoveries in the Whinchat does not allow such calculations for this species but, based on our present data, apparently only a small proportion of surviving males return to the breeding site of the previous year. These numbers imply that about 25% of survived Yellow Wagtails, about 70% of males and all females of Booted Warbler, and the majority of Whinchats nested somewhere outside the study meadow the summer following banding year. The majority of such birds might still have settle nearby the study meadow (Paradise *et al.* 1998). However, we surveyed all suitable habitats within several kilometers from the 20-ha study meadow, and indeed the nearest large grasslands were over 10 km from it. We suggest, therefore, that the majority of the surviving but non-returning adult birds nested at the distance of more than 10 km from the banding site. Our finding of a Whinchat male, recovered 43 km from the Chistii Dor banding station, may support this suggestion.

Our data suggest that species-specific local return rates and annual fluctuations in these rates are largely defined by the reproductive success in previous years, as shown for many other passerine species (Bollinger & Gavin 1989, Haas 1998, Hoover 2003, Newton 2003). Estimates based on nests with known fate show that the reproductive success of Yellow Wagtail was two times higher

than in the other two species, which can be consistent with a high local survival and return rate. After unsuccessful breeding of Yellow Wagtails in 2008, local survival (return) rates of both sexes decreased to zero and the local population virtually disappeared. However, causes that determine variation in reproductive success of the model species could not be evaluated using the present data.

The non-existence of recoveries of young individuals, born in the same meadow the previous year, suggests that in this study, the locally-born young individuals in the three species may rarely take part in forming the local populations. These populations thus mostly consist of individuals who were born outside the focal meadow. However, once successfully nested at the study meadow, Yellow Wagtails returned there with a high probability the following year. In some years all males and at least half of females appeared to be those who nested there the previous year. On the contrary, the populations of Whinchats and Booted Warblers were annually renewed. Our data on the age ratio of Whinchats indicate that, in years with high population density, more than 70% of males of unknown origin were at least three calendar years old, i.e., they had probably already bred outside the local population.

Our results also indicate that even small local population (5–7 pairs) of Yellow Wagtail can act as a source population in successful breeding years. After successful years, all survived adult birds returned to the previous-year nesting sites; the majority of the population thus appears resident. However, because of their small size such local populations appear to be unstable (Dale 2001). After unsuccessful years the residents may not return to the isolated patch, which leads to a decline or even local extinction of the population. In the other two species, the local populations of a given isolated meadow patch seem to renew almost entirely every year by immigrants of unknown origin, i.e., they serve as sink populations. These immigrants may not solely be first-time breeders, as shown for the Whinchat in this paper.

The high site-fidelity rate, demonstrated here for the Yellow Wagtail, is determined not only with isolation of the local population but with high habitat quality and high reproductive success. The increasing site-fidelity rate could be partly affected by high resighting probability within a

small, isolated territory, which was the case in the present study. Thus, spatial isolation of local populations of the three focal species may not limit natal and breeding dispersal, but dispersal range can be several tens of kilometers. Such a role of dispersal is described for a variety of migratory birds with patchy distribution (Hansson *et al.* 2002, Dale *et al.* 2005, Mayer *et al.* 2009). The present data suggest that the negative effects of living in isolated patches may be at least partially mitigated by natal and breeding dispersal.

Acknowledgements. The work in the Russian North National Park was made possible through the support of the administration of the park, particularly A. L. Kuznetsov and L. V. Kuznetsova. The students and graduates of the Department of Zoology and Ecology, Moscow Pedagogical State University (T. Makarova, S. Makushina, I. Malykh, M. Morozova, S. Pavlova and N. Pinchuk) were involved in the field work.

Pesimäpaikkauskollisuus ja levittäytyminen muuttavien varpuslintujen eristyneissä populaatioissa

Eristyneessä elinympäristöaikussa eläminen voi mm. lisätä paikallisen populaation sukupuuttoris-kiä, mutta tällaisia riskejä voidaan osin kompensoida nuoruus- ja pesimäajan levittäytymisellä. Tätä kysymystä tarkastellaksemme analysoimme viisivuotista pikkukultarinnan, pensastaskun ja keltavästäräkin (vastaavasti *Hippolais caligata*, *Saxicola rubetra* ja *Motacilla flava*) rengastusaineistoa 20 hehtaarin niittyalueella, jota eristää laaja metsäalue.

Rengastimme yksilöllisesti 203 pikkukultarinta-, 193 pensastasku- ja 83 keltavästäräkkiyksilöä. Rengastusta seuraavina vuosina neljä pikkukultarintakoirasta (2,0 %), yksi pensastaskukoiras (0,4 %) ja 11 keltavästäräkkiä (13,3 %; 7 koirasta ja 4 naarasta) palasi tutkimusniitylle. Keltavästäräkin paluuprosentti oli merkittävästi kahta muuta lajia korkeampi. Keltavästäräkin rengaskontrollimäärät vaihtelivat paljon vuodesta toiseen ja olivat yhteydessä edellisessä pesimämenestykseen: hyvää pesimäkesää seurasi usein kontrolli samassa paikassa seuraavana kesänä. Pesäpoikasina rengastettuja yksilöitä löydettiin seuraavina kesinä samalta paikalta äärimmäisen harvoin (kolme kaikkiaan 258:sta rengastetusta).

Näiden havaintojen pohjalta esitämme, että (1) lajikohtaiset paluuprosentit ja vaihtelu niissä riippuvat paljolti (kuolleisuudesta ja) edellisesän pesimämenestyksestä, ja (2) tutkittujen lajien paikallipopulaatiot koostuvat etupäässä ulkopuolelta paikalle tulleista (immigraatio): paikallista poikastuottoa ei näytetä merkittävästi rekrytoitavan populaatioon. Eristyneessä laikussa elämisen negatiivisia vaikutuksia voidaan säädellä poikas- ja pesimäajan levittäytymisellä.

References

- Anderson, D. R. & Burnham, K. P. 2002: Avoiding pitfalls when using information-theoretic methods. — *Journal of wildlife management* 66: 912–918.
- Baillie, S. R. & Peach, W. J. 1992: Population limitation in Palaearctic–African migrant passerines. — *Ibis* 134: 120–132.
- Bairlein, F. 1983: Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. — *Ornis Scandinavica* 14: 239–245.
- Bastian, H.-V. 1992: Breeding and habitat dispersal of whinchats *Saxicola rubetra*. — *Ringling and migration* 13: 13–19.
- Beier, P. & Noss, R. F. 1998: Do habitat corridors provide connectivity? — *Conservation Biology* 12: 1241–1252.
- Bollinger, E. K. & Gavin, T.A. 1989: The effects of site quality on breeding-site fidelity in Bobolinks. — *Auk* 106: 584–594.
- Brown, J. H. & Kodric-Brown, A. 1977: Turnover rates in insular biogeography: Effect of immigration on extinction. — *Ecology* 58:445–449.
- Butyev, V. T. & Ezhova, S. A. 1987: The population of the grassland birds society under the conditions of Middle-Taiga in Vologda region. — *Impact of the economic development of woodland areas of the European North on the population of animal world. M., "Nauka": 131–140. (In Russian)*
- Butyev, V.T., Shitikov, D.A. & Fedotova, S.E. 2007: Nesting biology of the Booted Warbler (*Hippolais caligata*, Passeriformes) at the northern boundary of its range. — *Zoological Journal* 86: 81–89. (In Russian with English summary)
- Clarke, A.L., Sæther, B.-E. & Røskaft, E. 1997: Sex biases in avian dispersal: a reappraisal. — *Oikos* 79: 429–438.
- Cramp, S. (ed.) 1988: *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. 5. Tyrant flycatchers to thrushes.* — Oxford University Press, Oxford. 1063 pp.
- Cramp, S., ed. 1992: *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. 6. Warblers.* — Oxford University Press, Oxford. 728 pp.
- Dale, S. 2001: Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. — *Oikos* 92: 344–356.
- Dale, S., Lunde, A. & Steifetten, Ø. 2005: Longer breeding dispersal than natal dispersal in the Ortolan Bunting. — *Behavioral Ecology* 16: 20–24.
- Donovan, T. M., Thompson, F. R. III, Faaborg, J. & Probst, J. R. 1995: Reproductive success of migratory birds in habitat sources and sinks. — *Conservation Biology* 9:1380–1395.
- Drost, V. R. 1948: Populationsstudien an der Englischen Schafstelze, *Motacilla flava flavissima* Blyth, auf Helgoland. — *Vogelwarte* 1: 18–28.
- Eliason, B. C. 1986: Female site fidelity and polygyny in the Blackpoll Warbler (*Dendroica striata*). — *Auk* 103: 782–790.
- Förschler, M. I., del Val, E. & Bairlein, F. 2010: Extraordinary high natal philopatry in a migratory passerine. — *Journal of Ornithology* 151: 745–748.
- Greenwood, P. J. 1980: Mating systems, philopatry, and dispersal in birds and mammals. — *Animal Behaviour* 28:1140–1162.
- Greenwood, P. J. & Harvey, P. H. 1982: The natal and breeding dispersal of birds. — *Annual Review of Ecology and Systematics* 13:1–21.
- Haas, C. A. 1995: Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. — *Conservation Biology* 9: 845–854.
- Haas, C. A. 1998: Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. — *Auk* 115:929–936.
- Hansson, B., Bensch, S., Hasselquist, D. & Nielsen, B. 2002: Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. — *Oecologia* 130: 536–542.
- Holmes, R. T, Marra, P. P. & Sherry, T. W. 1996: Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. — *Journal of Animal Ecology* 65:183–195.
- Hoover, J.P. 2003: Decision rules for site fidelity in a migratory bird, the prothonotary warbler. — *Ecology* 84: 416–430.
- Jenni, L, Winkler, R. 2004: *Moult and ageing of the European passerines.* — Academic press. 450 pp.
- Karr, J. R., Nichols, J. D., Klimkiewicz, M. K. & Brawn, J. D. 1990: Survival rates of birds of tropical and temperate forests: will the dogma survive? — *American Naturalist* 136: 277–291.
- King, J.R. & Mewaldt, L.R. 1987: The summer biology of an unstable insular population of White-crowned sparrows in Oregon. — *Condor* 89: 549–565.
- Korovin, V.A. 2004: *Birds in agricultural landscapes of Ural.* — Urals State University Publishing House, Yekaterinburg. 504 pp. (In Russian with English summary)

- Lande, R. & Barrowclough, G.F. 1987: Effective population size, genetic variation, and their use in population management. — In *Viable Populations for Conservation* (Soulé, M. E. ed.): 87–123. Cambridge University Press, Cambridge.
- Lanyon, S. M. & Thompson, C. F. 1986: Site fidelity and habitat quality as determinants of settlement pattern in male painted buntings. — *Condor* 88: 206–210.
- Lapshin, N.V. 2001: Peculiarities of Ladoga Lake islands colonization by passerines. — Intern. Konfer. “Biodiversity of the European North”, Petrozavodsk. 268 pp. (In Russian).
- Lawn, M.R. 1982: Pairing systems and site tenacity of the willow warbler *Phylloscopus trochilus* in Southern England. — *Ornis Scandinavica* 13: 193–199.
- Lebreton, J. D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992: Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. — *Ecological Monographs* 62: 67–118.
- Mayer, C., Schiegg, K. & Pasinelli, G. 2009: Patchy population structure in a short-distance migrant: evidence from genetic and demographic data. — *Molecular Ecology* 18: 2353–2364.
- Mayfield, H.F. 1975: Suggestions for calculating nest success. — *Wilson Bulletin* 87: 456–466.
- McClintock, B. & White, G. 2011. From NOREMARK to MARK: software for estimating demographic parameters using mark-resight methodology. — *Journal of Ornithology* 151. DOI 10.1007/s10336-010-0524-x. (In press)
- Mewaldt, L. R. & King, J. R. 1985: Breeding site faithfulness, reproductive biology, and adult survivorship in an isolated population of Cassin’s finches. — *Condor* 87: 494–510.
- Müller, M., Spaar, R., Schifferli, L. & Jenni, L. 2005: Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*). — *Journal of Ornithology* 146: 14–23.
- Newton, I. 2003: The speciation and biogeography of birds. — Academic Press, London-San Diego. 668 pp.
- Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. 1998: Patterns of natal and breeding dispersal in birds. — *Journal of Animal Ecology* 67: 518–536.
- Payevsky, V. A., Vysotsky, V. G., Yefremov, V. D., Markovets, M. Y., Morozov, Y. G. & Shapoval, A. P. 1997: Sex-specific survival rates in birds. — *Zhurnal Obshchei Biologii* 58: 5–20.
- Payne, R. B. 1991: Natal dispersal and population structure in a migratory songbird, the indigo bunting. — *Evolution* 45:49–62.
- Pitney Bowes MapInfo Corporate, 2007. Mapinfo Professional, version 9.0. <http://www.pb.com>
- Pulliam, H. R. 1988: Sources, sinks, and population regulation. — *American Naturalist* 132:652–661.
- Renner, H. M. & McCaffery, B. J. 2008: Demography of eastern yellow wagtails at Cape Romanzof, Alaska. — *Wilson Journal of Ornithology* 120: 85–91.
- Roth, R. R. & Johnson, R. K. 1993: Long-term dynamics of a wood thrush population breeding in a forest fragment. — *Auk* 110: 37–48.
- Saether, B.E. 1989: Survival rates in relation to body weight in European birds. — *Ornis Scandinavica* 20: 13–21.
- Schmidt, K. & Hantge, E. 1954: Studien an einer farbig beringten Population des Braunkehlchens (*Saxicola rubetra*). — *J. fur Ornithology* 95: 130–173.
- Sedgwick, J. A. 2004: Site fidelity, territory fidelity and natal philopatry in willow flycatchers (*Empidonax traillii*). — *Auk* 121: 1103–1121.
- Shitikov, D. A. 2000: Space-time structure of fauna and bird population of the European agricultural lands of northern Russia. — Ph. D. thesis, Moscow Pedagogical State University, Moscow. (In Russian)
- Shitikov, D. A. & Fedchuk, D. V. 2008: The role of territorial relations in the formation of the breeding population of Passerines in a forb meadow of the middle taiga. — *Zoologicheskij zhurnal* 87: 206–217. (In Russian with English summary)
- Shitikov, D. A., Fedotova, S. E. & Fedchuk, D. V. 2008: New data about site fidelity and philopatry rates of Booted Warbler (*Hippolais caligata*) in Vologda region. — *Ornithologiya*, 34 (2): 218–219 (In Russian)
- Siriwardena, G. M., Baillie, S. R. & Wilson, J. D. 1998: Variation in the survival rates of some British passerines with respect to their population trends on farmland. — *Bird Study* 45:276–292.
- Sokolov, L. V. 1991: Philopatry and dispersal in birds. — Moscow. 232 pp. (In Russian)
- Svensson, L. 1984: Identification guide to European passerines. — Author’s edition, Stockholm. 368 pp.
- Tiainen, J. 1983: Dynamics of a local population of the willow warbler *Phylloscopus trochilus* in Southern Finland. — *Ornis Scandinavica* 14: 1–15.
- Weatherhead, P. J. & Boak, K. A. 1986: Site infidelity in song sparrows. — *Animal Behaviour* 34: 1299–1310.
- Weatherhead, P. J. & Forbes, R. L. 1994: Natal philopatry in passerine birds: genetic or ecological influences? — *Behavioral Ecology* 5: 426–433.
- Wheelwright, N. T. & Mauck, R. A. 1998: Philopatry, natal dispersal, and inbreeding avoidance in an island population of savannah sparrows. — *Ecology* 79: 755–767.
- Wiens, J. A. 1969: An approach to study of ecological relationships among grasslands birds — *Ornithological monographs* 8: 1–93.
- Wittenberger, J. F. 1978: The breeding biology of an isolated Bobolink population in Oregon — *Condor* 80: 355–371.
- Zubcovsky, N. E, Matancev, V. A. & Tulkin, Y. A. 1989: To the study of philopatry of passerine birds in small communities — *Ekologiya* 4: 84–86 (In Russian)