

# BIRD POPULATION DYNAMICS IN RELATION TO HABITAT QUALITY

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The complexity of natural landscapes composed of habitats differing in quality, extent, and patchiness provides the adaptive environment needed to explain the reactions of species to contemporary man-made habitat changes. Long-term observations of patterns and dynamics in pristine communities and populations provide valuable information on those life history strategies which facilitate survival in the face of landscape fragmentation. Studies of adaptations to habitats are important as complex habitat conservation programs provide the most realistic way for species conservation. Analyses of 15-year data on the passerine bird community of Central Siberian taiga, including the numbers and distribution of breeding pairs over the whole local variety of habitats, are presented below.

## 1. Habitats

The study area was located on the Yenisei river banks, in the middle taiga subzone, and comprised 18 sampling plots, 450 ha in total. In general, they represented the following three habitat groups.

**TAIGA:** primeval coniferous forests covering about 40% of watersheds; as the zonal climax, it is quite uniform and widespread, but has a rather low biomass productivity; local climatic extremes are smoothed by the evergreen tree layer.

**BURNS:** secondary taiga derivatives, primarily young birch undergrowth with remains of burnt conifers; they include differently aged deciduous and mixed stands, and cover more than half of the territory; they are quite productive due to destroyed moss cover and recycling of nutrients, but they are not protected against climatic perturbations.

**FLOOD-PLAIN:** wide band along the Yenisei riverside; it comprises various luxuriant vegetation types composing the alluvial succession series: Overgrowing lakes, flood meadows, willow thickets, shrubs, and multi-layered mixed forests; it is very patchy, has a high biomass and productivity, but is affected by flood regimes.

Other habitats constitute scarce small patches of open areas like bogs, beaches, and settlement surroundings - strange for the taiga zone but important for various allochthonal faunistic elements penetrating into the taiga.

TABLE 1. Average annual assemblage structure indices. Total density was estimated on 4 ha sampling plots censused 9-15 years each; species diversity was sampled in the same areas divided into  $\kappa$  fragments containing on average 25 breeding pairs each. Density is expressed in pairs per 4 ha. Diversity and its components were calculated according to the Shannon-formula (Muhlenberg 1993).

Habitat type	<i>n</i>	Density		<i>k</i>	Diversity		Richness		Evenness	
		Mean	SD		Mean	SD	Mean	SD	Mean	SD
Taiga	13	5.0	0.7	5	1.90	0.17	2.47	0.35	0.88	0.03
Burns	15	9.4	1.8	8	1.89	0.20	2.69	0.35	0.84	0.04
Flood-plain	6	19.1	7.9	6	2.41	0.09	3.85	0.28	0.93	0.02

## 2. Habitat Niche Structure

Considering the bird assemblage structure of the three habitat types (Table 1), we find the bird density gradually increasing in accordance with habitat productivity (Bourski 1995). Nevertheless, the species diversity is generally equal in taiga and burns regardless of productivity. There is a constant set of common species forming taiga assemblages. The same species are present on burns in low numbers, but in addition, there are a small number of specialist burns species with high abundances. Thus, whereas taiga assemblages reach their diversity mostly through higher evenness, having many constant inhabitants, burn complexes are rather uniform. Their richness depends on the amount of trees and tree patches left unburnt.

By attributing each species to its preferable (most densely populated) habitat type, one can easily see a striking contrast between the ratio of habitat types in the area (Figure 1 A) and in breeding passerine species preference (Figure 1B). Mature dark coniferous forests cover a large part of the area, and the taiga group comprises 16 species out of 66. At the same time, there are about two times more species specialized on flood-plain vegetation complexes, and about two times less species selecting burns as a preferred habitat type, despite the area of burn habitat being ten times greater. Thus, neither the large area of pyrogenic succession, nor the higher productivity of burns create conditions favourable for fine specialization.

To check the species-habitat relationship in the community, averaged extensive long-term data on bird distribution was treated in a spatial niche structure analysis. The initial matrix of 66 species breeding densities over 53 habitats (summarily making up the three main habitat types) was expanded according to the importance of each habitat as a peculiar resource distinguished by birds. That is, each habitat was weighed as much as it differs from other habitats or contributes to the overall spatial heterogeneity of the bird community. On the basis of the expanded matrix, information measures of niche breadth and overlap were calculated (see Colwell & Futuyma 1971 for more details).

To appreciate species grouping in relation to habitat, one needs to analyse the multidimensional structure, where the species located close to each other in multidimensional space defined by habitat variables have high niche overlap. By means of multidimensional scaling technique (Kruskal & Wish 1978), the multidimensional structure can be converted into a two-dimensional one, like the principal structure of a complicated molecule can be shown on a sheet plane (Figure 1C). Despite small inevitable distortions

on, the method orders species corresponding to their similarity in niche space. Species with similar habitat preferences should be located together, species with quite different habitat preferences should be at the extremes of the distribution, and species similar to most of the others should be near the centre. The axes can be interpreted as forming an "ecological space" of habitat preferences reflecting species similarity or dissimilarity.

The partitioning of this space (Figure 1C) shows the flood-plain species as the more specialized ones. They have the lower niche breadth and are grouped mainly aside, at the periphery of ecological space. Taiga species rarely have such narrow niches, but they are more restricted to this habitat type (the distance from the origin is greater,  $a = 0.009$ ), and they cannot use dissimilar habitats. On the contrary, habitat niches of the burn birds are wider than for the flood-plain ( $a < 0.001$ ) and the taiga species ( $a = 0.159$ ) and closer to the origin ( $a = 0.015$  and  $0.001$ , respectively), which should mean high habitat tolerance, generalism in habitat selection, opportunistic strategies to share almost any habitat niche, wherever and whenever it is not saturated by more fitting inhabitants. Therefore, instability patterns of different species groups were analysed.

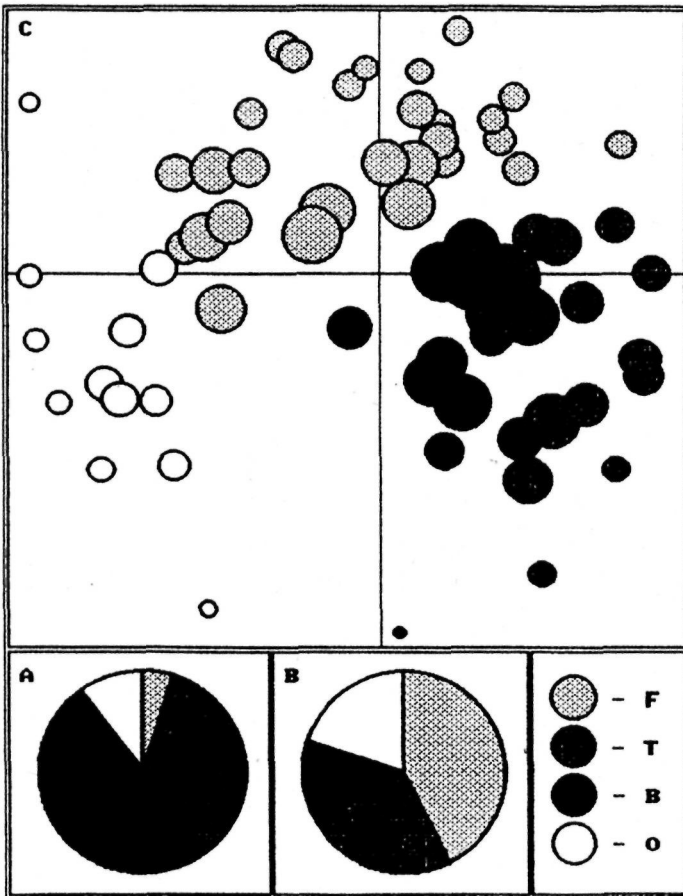


Figure 1. Habitat niche structure. A. Proportions of the habitat types in nature. B. Proportions of species of breeding passerines grouped according to their preferred habitat. C. Habitat niche breadth (diameter of circles) and overlap (closeness) of 66 passerine species. Habitat types: F - flood-plain, T - taiga, B - burns, O - others. See text for more explanation.

### 3. Population Instability Patterns

Population stability patterns were investigated by regressing the mean annual number of breeding pairs against the year-to-year variation of breeding numbers, expressed as coefficient of variation. The parameter  $a$  (coefficient of intercept) estimates average variation at the scale of a single breeding territory. It reflects the spatial instability or instability of habitat distribution. In the case of complete occupancy of a habitat, the allocation of breeding pairs is managed by territoriality. Therefore, the variation is usually much lower than expected at random in optimal habitats saturated every year. The variation in marginal habitats is about random level as far it reflects free distribution over free space. If year-to-year differences make habitats unsuitable in some years, then the variation will increase.

Successively joining populations reduces the coefficient of variation as this removes variation in habitat choice. For instance, birds may shift to open forests with early melting snow cover on slopes when spring is late. However, yearly fluctuations in weather is less likely to influence the breeding numbers on a plot including both the slopes and the foot of a hill. On the other hand, synchronized fluctuations of numbers caused by large-scale external factors almost always exceed random level. The parameter  $b$  (regression coefficient) expresses this temporal instability irrespective of population size and habitat distribution.

The two components of population instability were obtained for 28 common species representing over 92% of the local community. Taiga species, such as *A. hodgsoni* RICHMOND, 1907, show the most constant breeding habitat distribution: high stability in use of many particular sites. Small fluctuations are more or less synchronous eve-

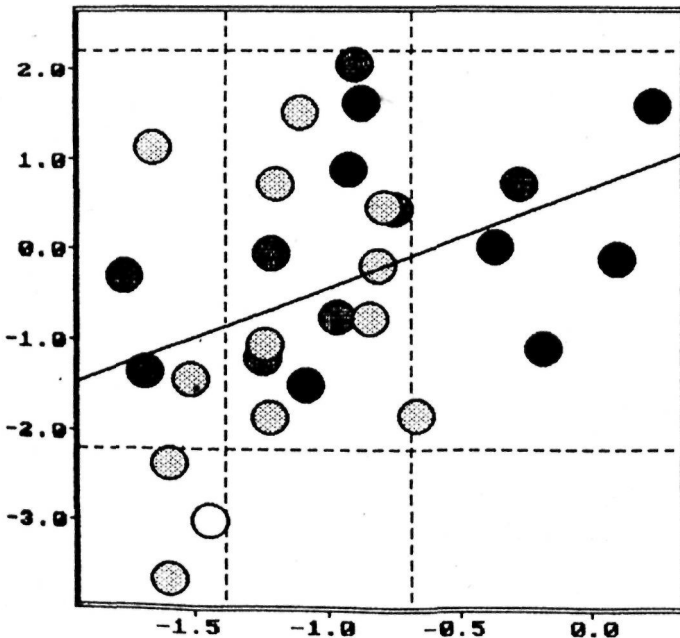


Figure 2. Population long-term trend versus variation. X-axis: annual variation as  $\log(\text{CVrc})$ , where  $\text{CVrc}$ : trendless coefficient of variation of breeding numbers corrected by Svensson's (1978) method. Y-axis: Student's  $t$ -value testing significance of long-term population increase or decrease. Particular species are shown by dots filled as for Figure 1. Rare species are excluded. Dashed lines indicate lower and upper limits of random changes at  $\alpha = 0.05$ .

rywhere; so the temporal instability component is large. Flood-plain species have the most stable populations in general. This is reached by compensatory density changes in fragments of different quality, at the medium level of spatial stability. Burns inhabitants are notable for both the components, spatial and temporal, being the highest. Among them, insectivorous species such as *Phylloscopus inornatus* (BLYTH, 1842) have extremely unstable numbers in most habitats besides the optimal one. Seed-eaters such as *Acanthis flammea* (LINNAEUS, 1758), in general, do not settle down anywhere twice in consecutive years. In both cases, the more samples that are taken, the more significant fluctuations are evident: local numbers strongly depend on the broad-scale movements of mature birds.

TABLE 2. Relative amount of repeatedly captured individuals and return ratio for selected species in a 50-ha flood-plain study plot during five years of netting and ringing. Return ratios were calculated as the proportion of repeatedly captured individuals which were recorded the following year, without any correction, and do not mean site tenacity only. Poorly represented species are omitted. \* including numerous immigrants for moulting period.

Species name	Censused nesting individuals	Recaptured individuals		Next year return (%)	
		adults	immatures	adults	immatures
Flood-plain species:					
<i>Sylvia curruca</i>	168	115	26	30	0
<i>Luscinia calliope</i>	162	111	58	27	9
<i>Zoothera sibirica</i>	160	108	83	45	13
<i>Phylloscopus borealis</i>	154	76	19	25	21
<i>Locustella certhiola</i>	102	24	2	8	0
<i>Acrocephalus dumetorum</i>	100	47	7	9	14
<i>Phylloscopus collybita</i>	100	39	49	54	24
<i>Emberiza aureola</i>	78	36	8	42	25
<i>Turdus iliacus</i>	70	32	53	19	17
<i>Turdus pilaris</i>	64	18	31	39	23
<i>Emberiza schoeniclus</i>	62	30	25	57	48
<i>Luscinia svecica</i>	46	28	30	39	13
<i>Carpodacus erythrinus</i>	40	14	3	43	33
<i>Phylloscopus fuscatus</i>	32	20	10	35	30
Taiga species:					
<i>Parus montanus</i>	112	12	21	33	10
<i>Pyrrhula pyrrhula</i>	30	6	8	33	13
<i>Sitta europaea</i>	22	6	34	50	21
<i>Turdus obscurus</i>	4	5	9	20	11
Species of burns:					
<i>Fringilla montifringilla</i>	134	60	13	2	0
<i>Phylloscopus inornatus</i>	80	25	18	0	0
<i>Turdus ruficollis</i>	52	85*	104*	49*	13*
<i>Ficedula parva</i>	24	20	49	0	0
<i>Acanthis flammea</i>	12	7	0	0	—
<i>Emberiza pusilla</i>	12	7	23	0	0

#### 4. Long-term Trends

The annual bird census data were regressed over the 15-year study period to analyse population trends. In contrast to European studies (Payevsky 1985), very few species show any real decrease or increase of their total numbers. A great majority of the trends remains still within the confidence limits of random fluctuations confirming a low level of ecological disturbance in Central Siberian ecosystems (Bourski 1994). Nevertheless, some tendencies were noted when particular species, groups, or traits were considered. For example, species with a higher variability in population size, especially those of burns, tended to increase (Figure 2), whereas the species of taiga and flood-plain habitats with relatively constant numbers tended to decrease. The significance level of the dependence increases up to  $\alpha = 0.02$  when all 66 species are taken together.

#### 5. Site Tenacity

Data of marked birds was used to estimate a relationship between population stability and site tenacity (Table 2). Avoiding the complicated problem of separating dispersal and mortality, only actual data is presented. It appears to be appropriate for a rough comparison keeping in mind the annual survival rate for passerines is nearly 50% in adults and 20 - 30% in young (Payevsky 1985).

It is difficult to sample taiga birds effectively by mist-netting because they dwell in tree canopies. Nevertheless, all four taiga species show a site tenacity, despite the study plot representing sub-optimal habitat. Most of *P. montanus* CONRAD, 1827 and *S. europaea* LINNAEUS, 1758 territories were occupied permanently for several years starting at an age of 1 - 1.5 months. The same was found for *Nucifraga caryocatactes* (LINNAEUS, 1758). Indirect observations indicate strict site tenacity for *Phylloscopus proregulus* (PALLAS, 1811), *A. hodgsoni*, and *Muscicapa sibirica*, which do not breed outside taiga habitats. *Tarsiger cyanurus* is probably an exception.

There is a clearly contrary picture for species of burns: most of them show a lack of site fidelity. At the same time, there is evidence that they can imprint the territory. So a female *F. montifringilla* LINNAEUS, 1758 ringed when moulting was found breeding two years later. A nestling *E. pusilla* PALLAS, 1776 marked in the nest was recognized the next spring before breeding but not later. Similar results were found on burns for *P. inornatus*: It forms dense settlements of 10 - 50 pairs; territorial pairs appear at the same place the next spring, but for several days only, then disappear completely, and a settlement is founded on a new place. A high fidelity was found in a *T. ruficollis* PALLAS, 1776 flood-plain sub-population, but it applied mostly to the post-breeding moulting sites.

In flood-plain birds, a philopatry is expressed just as in taiga species. However, some species of the earlier alluvial succession stages are less philopatry due to the insular distribution of their habitats and the environmental instability caused by floods. Their population size is also less stable, breeding time is delayed, imprinted area seems to be sufficiently larger, and habitat selection takes place in spring: before breeding or **even** instead of it.

## 6. Discussion

Species preferring a certain habitat type have a set of common adaptive tendencies despite their taxonomic heterogeneity, though the way to reach the same result differs considerably depending on foraging, migratory and other specific traits. Adaptations to habitat type are more clearly expressed in invertebrate consumers whose relation to habitat is more integral in that their feeding adaptations should fit specific foraging sites, rather than any particular prey item (Lack 1971). Invertebrate consumers of the taiga habitat type use scarce food resources which suppose generalization in foraging sites as well (Recher 1990). That is why we are unlikely to find among them two congeners together in one habitat. However, relative microclimatic stability provided by phytocenotic development, and the vast area of taiga lead to specialization on particular habitats. Territoriality plays an important role as a way of spacing and large territories allow compensation of low resource availability (Fretwell & Lucas 1970). Site tenacity increases an individual's familiarity with an area. It would be more beneficial in uniform habitats, as the profits of finding a better territory do not repay the expenses of the search. It is also common that individuals dwell in the same habitat after breeding until long-distance migration starts. All this leads to high ecological saturation, resource utilization efficiency, and spatial stability. Temporal population fluctuations depend mostly on the balance between reproduction and mortality affected by the local conditions.

High productivity and structural diversity but restricted area of flood-plain habitats suggest a fine specialization of flood-plain species relatively high densities but low total population sizes. Species diversity, despite its highest level, seems to be limited by floods and the small size of some habitat patches. Otherwise, one would expect to see in Figure 1C some more flood-plain species, more distant from the common centre. The patchiness promotes territoriality as a mechanism for establishing a territorial structure and density limitation (Fretwell & Lucas 1970). The influence of unpredictable floods on habitat conditions can be compensated for by opportunistic changes in habitat choice within the limited area which is used in a tenacious way. Seasonal habitat changes are characteristic as well. They are advantageous due to habitat patchiness and a wide variety of seasonally abundant food for which no additional specialization is required. It helps some species to prolong their stay within the breeding area and to allocate less time to winter quarters. Generally, habitat diversity in a flood-plain maintains a diversity of life histories, particularly including an additional dispersal with searching for a new site at a mature age [apparently in *5. curruca* (LINNAEUS, 1758), *Locustella* and *Acrocephalus* species]. The habitat richness and their complementary use maximizes the temporal stability of populations.

Sharp seasonality of the bioproductivity of secondary forests on burns, more rigorous microclimatic conditions, relatively fast successional changes, and probably irregular outbreaks of insects, create sufficient and unpredictable changes of habitat suitability. Insular distribution of particular restoration stages involves a spatial unpredictability. Such conditions favour a life history strategy to get all the required resources from one site, that is, to generalized foraging behaviour. Social behaviour develops side by side with remaining breeding territoriality, which leads to clumped ("Allee's ideal free");

Fretwell & Lucas 1970) distribution over a uniform habitat. Maintenance of old territories cannot guarantee its former quality, so that benefits of an annual search for a better site and seasonal habitat change exceed the costs of searching, and site fidelity is not obligatory any more. Nevertheless, birds like *T. ruficollis* show strong fidelity to moulting sites in flood-plains, and other species of burns also imprint a site in some cases (see above). Probably, during the imprinting process, a relationship with a set of successively changed sites is set up. If such a relationship remains fixed with benign (though not necessarily breeding) habitats, then local conditions are much more important for a final choice regarding unpredictable habitats. Local fluctuations of numbers are the greatest. They are caused by opportunistic movements and balance each other in a more general, geographic scale only. A similar dynamic pattern is also suggested for *Lullula arborea* populating early successional stages of pine forests in Central Europe (Rothhaupt & Vogel this volume: 230-236). Thus, habitat conditions of burns do not support habitat saturation and high efficiency of resource utilization, but facilitate development of high mobility and habitat tolerance.

Tree seed consumers, switching to insects at the seasonal peak of their availability, relate to a habitat mostly through adaptation to foraging tree species. Their food specialization, in general, promotes an increase in mobility and a decrease of local population stability, though these tendencies differ between birds of taiga climax vegetation and of pyrogenic successional series. Food items of the former are less accessible but larger and contain more energy. This favours seed storage and long-term use, all-year-round territoriality and site fidelity, complex resource utilization over the territory (gathering abundant insects, extraction of resting insects), as well as invasions following irregular seed crops: Seed-eaters of secondary forests are more notable for nomadic movements and a lack of attachment to any site. Thus, among seed-eaters, taiga species are also distinguished by site tenacity from species preferring burns. Species of both taiga and burns are represented in flood-plains. Because of a high diversity of foraging plants, and the higher and more regular availability of seeds, population fluctuations of seed consumers in flood-plains are rather smoothed.

## 7. Conclusions

Under conditions of landscape fragmentation, the survival of taiga species will be placed at risk because of their strong site tenacity, constant habitat choice, and considerable population fluctuations. Besides this, taiga species appear more sensitive to habitat quality changes and minimal size of fragments. The situation for many of the flood-plain species seems more dangerous because of restricted area and the higher economic value of their habitats. Existing flexibility of breeding habitat choice promotes a population's persistence only while this choice is possible within the local area. Dispersal abilities of some flood-plain species can be somewhat higher than those of taiga birds, but only to a degree similar to the natural separation of their habitats. Species of burns, which have much broader habitat tolerances, generally seem to be more persistent to landscape fragmentation and able to replace specialized taiga and flood-plain species in sufficiently rich fragmented habitats. Less productive taiga habitats will likely lose their



most specialized inhabitants. Artificial prevention of forest successional changes could threaten species of burns as well.

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